T6: MODELLING METHODS AND FINDINGS

A report provided to the Australian Government by the Reef Restoration and Adaptation Program

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September 2019

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This report should be cited as:

Anthony KRN, Condie S, Bozec Y-M, Harrison D, Gibbs M, Baird M, Mumby PJ, Mead D (2019) Reef Restoration and Adaptation Program: Modelling Methods and Findings. A report provided to the Australian Government by the Reef Restoration and Adaptation Program (112 pp).

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Acknowledgement

This work was undertaken for the Reef Restoration and Adaptation Program, a collaboration of leading experts, to create a suite of innovative measures to help preserve and restore the Great Barrier Reef. Funded by the Australian Government, partners include: the Australian Institute of Marine Science, CSIRO, the Great Barrier Reef Marine Park Authority, the Great Barrier Reef Foundation, The University of Queensland, Queensland University of Technology and James Cook University, augmented by expertise from associated universities (University of Sydney, Southern Cross University, Melbourne University, Griffith University, University of Western Australia), engineering firms (Aurecon, WorleyParsons, Subcon) and international organisations (Mote Marine, NOAA, SECORE, The Nature Conservancy).

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1. PREAMBLE

The Great Barrier Reef

Visible from outer space, the Great Barrier Reef is the world's largest living structure and one of the seven natural wonders of the world, with more than 600 coral species and 1600 types of fish. The Reef is of deep cultural value and an important part of Australia's national identity. It underpins industries such as tourism and fishing, contributing more than $6B a year to the economy and supporting an estimated 64,000 jobs.

Why does the Reef need help?

Despite being one of the best-managed coral reef ecosystems in the world, there is broad scientific consensus that the long-term survival of the Great Barrier Reef is under threat from climate change. This includes increasing sea temperatures leading to coral bleaching, ocean acidification and increasingly frequent and severe weather events. In addition to strong global action to reduce carbon emissions and continued management of local pressures, bold action is needed. Important decisions need to be made about priorities and acceptable risk. Resulting actions must be understood and co-designed by Traditional Owners, Reef stakeholders and the broader community.

What is the Reef Restoration and Adaptation Program?

The Reef Restoration and Adaptation Program (RRAP) is a collaboration of Australia's leading experts aiming to create a suite of innovative and targeted measures to help preserve and restore the Great Barrier Reef. These interventions must have strong potential for positive impact, be socially and culturally acceptable, ecologically sound, ethical and financially responsible. They would be implemented if, when and where it is decided action is needed and only after rigorous assessment and testing.

RRAP is the largest, most comprehensive program of its type in the world; a collaboration of leading experts in reef ecology, water and land management, engineering, innovation and social sciences, drawing on the full breadth of Australian expertise and that from around the world. It aims to strike a balance between minimising risk and maximising opportunity to save Reef species and values.

RRAP is working with Traditional Owners and groups with a stake in the Reef as well as the general public to discuss why these actions are needed and to better understand how these groups see the risks and benefits of proposed interventions. This will help inform planning and prioritisation to ensure the proposed actions meet community expectations.

Coral bleaching is a global issue. The resulting reef restoration technology could be shared for use in other coral reefs worldwide, helping to build Australia's international reputation for innovation.

The $6M RRAP Concept Feasibility Study identified and prioritised research and development to begin from 2019. The Australian Government allocated a further $100M for reef restoration and adaptation science as part of the $443.3M Reef Trust Partnership, through the Great Barrier Reef Foundation, announced in the 2018 Budget. This funding, over five years, will build on the work of the concept feasibility study. RRAP is being progressed by a partnership that includes the Australian Institute of Marine Science, CSIRO, the Great Barrier Reef Foundation, James Cook University, The University of Queensland, Queensland University of Technology, the Great Barrier Reef Marine Park Authority as well as researchers and experts from other organisations.

2. EXECUTIVE SUMMARY

This study presents the results of environmental and biological/ecological models and analyses to underpin the RRAP investment case. Here, we addressed three key questions: What are the likely trajectories of coral condition on the Great Barrier Reef under climate change without RRAP interventions? Can RRAP interventions help improve the outlook for Reef coral condition? If so, what is the scope for these interventions to deliver benefits in space and time? We examined the potential of three example RRAP interventions to improve the outlook for coral condition under climate change: rubble stabilisation, Reef-wide cooling and shading and assisted thermal adaptation of corals. Further, we explored the importance of additional crown-of-thorns starfish control because crown-of-thorns starfish are a major driver of coral mortality on the Reef. While the models we used are currently the best available, they continue to be refined and validated. Results should thus be regarded as preliminary, with improvements expected as RRAP evolves over the next few years.

Projected trajectories for the Reef under best-practice conventional management, but without new interventions, were characterised by overall decline of coral cover. Under moderate climate change, represented by the Representative Concentration Pathway (RCP) 2.6 adopted by the Intergovernmental Panel on Climate Change, coral cover was projected to stabilise and potentially show recovery after 2050 as surviving, and naturally warm-adapted, corals gain abundance. The extent to which coral cover is expected to decline or recover in the absence of additional interventions will be contingent on the capacity of corals to adapt naturally to warming. A tendency for stronger adaptation in the southern Great Barrier Reef suggests connectivity may interact with adaptation to drive spatial patterns of coral recovery. Under severe climate change (RCP 8.5), the models projected strong and precipitous coral decline, with coral cover likely to fall below five percent by 2075. Natural adaptation could buy time for sustained coral condition in the coming decades under RCP 8.5, but would be followed by steep decline after 2050.

Simulating Reef-wide solar radiation management (specifically assuming that cloud brightening using salt spray is the delivery mechanism) in combination with the simulated outplanting of warm-adapted corals and simulated suppression of crown-of-thorns starfish outbreaks, indicated a potential to markedly improve coral trajectories under both climate change scenarios. Of the three interventions, outplanting of warm-adapted corals showed the lowest efficacy: 100 million enhanced corals added to 100 reefs per year only marginally improved coral cover on 10-200 reefs.

A key finding was that the efficacy of interventions deployed in combination was greater than the sum of individual efficacies, particularly for solar radiation management combined with additional crown-of-thorns starfish control. Under RCP 2.6, the projected trajectory of this intervention strategy was one of improved and sustained coral condition to levels higher than present. Under RCP 8.5, the strategy would improve coral cover significantly in the near to mid-term (2050), but with eventual Reef-wide decline as severe warming under this scenario eventually exceeds the capacity of solar radiation management to provide cooling and limits for biological adaptation. The efficacy of rubble stabilisation depends on several factors including coral cover, availability of substrate for recruitment, disturbance regime and warming scenario. The scope for rubble stabilisation to improve the outlook for Reef coral cover is significant under RCP 2.6, but not under RCP 8.5.

This modelling study integrates available modelling tools for the Great Barrier Reef to address the question: what scope do new and existing management interventions have in sustaining coral condition under climate change? We emphasise that several limitations and caveats will affect how results can inform decision making now and in the subsequent RRAP R&D Program.

First, we do not provide complete assessment of uncertainties around how corals will respond to the suite of possible interventions that can enhance thermal tolerance, limiting our conclusions and recommendations around the full scope and risks of this intervention. While the local-scale model accounted for rates of natural adaptation and the role of heritability and dissemination of traits at the gene level, the Great Barrier Reef-wide model used a coarser-scale assessment that could not account for adaptation. Consequently, our system-wide projections in this study could not fully characterise the scope for coral populations to remain resilient under climate change.

Second, we did not formally model risks of new interventions. Real risks include the likelihood of pathogen spread from assisted gene flow, potentially leading to disease outbreaks. Other risks of assisted coral adaptation include the likelihood that a highly tolerant genotype becomes invasive. While this may be a positive outcome under expectations of dramatic coral decline (e.g. for warming >2°C), it becomes a significant risk under more benign scenarios where good coral condition and species diversity could have been sustained (e.g. warming <1.5°C). Risks of solar radiation management are not accounted for in the models. These include shading effects on deep (mesophotic) reefs and potential changes to Queensland weather. Largely, risks of preventing crown-of-thorns starfish outbreaks are not accounted for, partly because we model this intervention as hypothetical only. If one intervention candidate to prevent starfish outbreaks is a gene drive, then the full suite of risk implications of this avenue needs to be considered.

While acknowledging this suite of caveats, we see this modelling study as a first and critical step in a ‘value of information’ approach to understanding the critical uncertainty associated with new interventions. It helps us ask: what uncertainty do we need to reduce, to best inform RRAP decision making? Importantly, this study is insufficient to guide investment in specific intervention strategies. However, it provides new insight into the scope for new interventions to sustain coral condition under climate change, provided: (1) that such scope can be realised via an effective R&D program followed by cost-effective and timely deployment, (2) that downside consequences are manageable and exceeded by benefits, and (3) that deep uncertainty and circumstances not accounted for will not overwhelm those benefits. Although the Great Barrier Reef is the world’s largest coral reef ecosystem in a complex socio-economic setting, the RRAP challenge of seeking solutions that produce sustained benefits in a landscape of risk and uncertainty is no different from the ongoing challenges of making investment decisions in a financial market in flux.

3. INTRODUCTION, BACKGROUND AND OBJECTIVES

Models are required to understand how ecosystems respond to environmental impact and to identify effective management intervention. For a complex ecosystem like the Great Barrier Reef, under pressure from global and local stressors, the demand on models to identify effective management solutions that reconcile multiple values and risks is growing. The overall purpose of this project is to explore, using tailored environmental and ecological models, how new interventions on the Great Barrier Reef might help sustain coral condition under climate change.

This report describes how modelling in the Reef Restoration and Adaptation Program (RRAP) Concept Feasibility Study informs the scope for a small set of RRAP interventions to sustain or increase the condition of corals on the Great Barrier Reef. The project combines the skills of a suite of simulation models to support the feasibility assessment. There were five specific objectives associated with this modelling project:

1. Link simulation models within a drivers-pressures-state-impacts-response framework to map how stressors and interventions combine to impact on reef condition and, via a linked project, reef values.
2. Understand how coral condition is expected to change under
    a. Moderate and severe climate change scenarios
    b. Best-case conventional management
    c. Assumptions of natural adaptation to warming.
3. Examine how an exploratory set of three new representative interventions may affect the expected trajectories of coral condition:
    a. Regional solar radiation management
    b. Assisted adaptation of corals to warming
    c. Rubble stabilisation.
4. Explore whether additional crown-of-thorns starfish control can enhance the efficacy of new interventions.
5. Estimate the consequences (with uncertainty) of these example interventions separately and in combination in space (>2000 reefs) and time (2020 to 2075).

In the concept feasibility stage of RRAP, we limit the modelling to a showcase of how a subset of representative interventions are likely to perform in sustaining coral condition under different climate change scenarios. In the next stage of RRAP (the R&D program), we will link modelling within an integrated decision-support system that transparently informs choices to develop, dismiss or undertake further research on interventions based on their performance against a suite of environmental, ecological, social, economic and cultural objectives. The environmental and ecological modelling presented here, in combination with analyses of economic benefits and costs (**T9—Cost-Benefit Analysis** and **T10—Benefit Streams**), represent the first step in informing a structured decision-making process charged with identifying new intervention strategies that can be effective in sustaining Great Barrier Reef values under environmental change, risk and uncertainty.

3.1 Document structure

We briefly review the environmental pressures on the Reef, their global, regional and local drivers, how they have played out in recent history, and how they are likely to play out in the future under climate change. We then outline our general modelling approach and provide a summary of the current RRAP model architecture in terms of how environmental, biological and ecological models are linked within a drivers-pressures-state-impact-response framework. The framework we use here is consistent with that used in Reef 2050 Long-term Sustainability Plan and the Reef Integrated Monitoring, Modelling and Reporting Program (RIMRep).

To inform intervention strategies under environmental change, reef managers and environmental policymakers are faced with four increasingly pressing questions:

1. What are the projected trajectories of the Reef ecosystem under different scenarios of climate change with continuation of best-practice conventional management?

2. To what extent could new intervention strategies, combined with conventional management, help sustain or improve Reef coral condition under climate change?
3. What are the risks associated with different intervention strategies compared with the status quo?
4. How could/should new interventions be combined in time and space to maximise benefits and minimise risks?

This report primarily addresses questions one and two for the purpose of informing the RRAP business case. It does so by integrating information from a suite of models, including climate models, eReefs models, and spatially explicit reef environmental and ecological models further developed within this project to explore the scope of a set of new interventions. Questions three and four will be central to the combined modelling and decision support strategy under the RRAP R&D Program.

In addressing questions one and two we explain how a set of interventions, used here as examples only and chosen in consultation with the RRAP Interventions group, are modelled to produce predictions of coral condition in space and time under different simulated RRAP strategies (including the no-RRAP case) and climate change scenarios. Their purpose is to provide quantitative estimates of ecological benefits of interventions, their consequences for benefits streams, and demonstrate how these ultimately inform cost-benefit analyses of these interventions.

Predictions of reef health and condition should ideally involve estimates of a comprehensive suite of reef vertebrates, invertebrates and microbes; however, we limit the scope of our analyses to predictions of coral condition only. We do this partly because (1) corals provide reef structure and essential habitats for other reef taxa, (2) most RRAP interventions explored in this feasibility study have a coral focus, and (3) because coral condition is an area of strength for available reef ecosystem models.

The results of modelling the impact of location-specific (individual reef) interventions such as reflective surface films and cool water injections are presented in separate reports (**T12—Cool Water Injection** and **T13—Ultra Thin Surface Films**).

3.2 Understanding the counterfactual – the future of Reef corals without RRAP

Addressing question one is about understanding the counterfactuals – i.e. the possible, alternative, forward-projection scenarios of Reef coral condition in the absence of RRAP. Counterfactuals for different climate change scenarios provide the essential basis against which to assess the likely benefits and risks of RRAP, as well as benefits versus risks of inaction. Modelling counterfactuals for different climate change trajectories is complex because it requires resolving how the suite of conventional management interventions will interplay with climate change to produce patterns of coral condition in space and time. This means resolving how water quality, temperature, connectivity and other environmental variables will interact to drive the dynamics of coral assemblages in the Reef system. In addition to these environmental effects, the population dynamics and predatory influence of crown-of-thorns starfish, a major driver of coral mortality on the Reef (De'ath et al. 2012), need to be understood, including how they can be controlled by interventions.

Two critical, and linked, questions are emerging in a time of climate-driven coral decline on the Reef and worldwide. First, to what extent will corals adapt naturally to environmental change (Berkelmans and van Oppen 2006; Howells et al. 2011; Frieler et al. 2012; Logan et al. 2014)? Second, what is the role of best-practice (or intensified) conventional management in laying the foundation for new interventions (e.g. Anthony et al. 2017)? As addressing these questions is a prerequisite for exploring the scope of new interventions, we give significant attention to understanding the RRAP counterfactual, both for the environmental and ecological/biological models.

3.3 The role of new interventions

We address question two, to what extent can new intervention strategies improve outcomes, by focusing on an example suite of interventions. These were selected as being representative of the variety of intervention types being considered within RRAP. Preliminary assessment showed these had promise in terms of their efficacy across a range of scales. The purpose of this set of preliminary interventions was to explore the scope of intervention strategies – i.e. what ecological benefits could arise should such a scenario prove to have efficacy. The economic benefits arising from ecological benefits are addressed specifically in a separate report (**T10—Benefit Streams**). Importantly, the purpose was not to produce specific intervention recommendations for future deployment, but simply to explore the potential of interventions more broadly by assessing benefits across a set of alternative scenarios of future Reef conditions.

Because the purpose of the RRAP Concept Feasibility Study is to understand the potential for interventions to sustain coral condition, we did not include the risks of interventions in the analyses at this time (question three). This omission includes: the risk of spreading disease with coral translocations (Hoegh-Guldberg et al. 2008; Aitken and Whitlock 2013), the risk that solar radiation management systems might fail after decades of operation (Matthews and Caldeira 2007), risks of ecosystem disruptions following the introduction of warm-adapted (and potentially competitively superior) genotypes/phenotypes (Ricciardi and Simberloff 2009), and unknown consequences of completely suppressing crown-of-thorns starfish outbreaks on the Reef. While these risks are likely to be significant, comprehensive modelling of detailed risk assessments of interventions was beyond the scope of this study. Importantly, however, a declining trajectory of coral condition under the status quo (counterfactual) itself represents significant risk – that is, the risk associated with not considering new interventions while the window of opportunity is closing (Anthony et al., 2017). Conversely, investing in costly interventions that do not convincingly demonstrate the scope to sustain coral condition also represent a form of risk associated with drawing resources away from other alternatives. In Appendix **B1** and **B2** we discuss the assumptions, caveats and limitations around how each intervention was modelled, to give the reader a sense of how representative modelling results are of reality, and what modelling improvements need consideration during the RRAP R&D Program.

Finally, spatial and temporal adaptive strategies to maximise intervention efficacy (question four) were not systematically modelled. However, by exploring a systematic design of three example interventions—separately and in combination—we were able to assess the extent to which these interventions synergise when combined. Also, we used a general modelling strategy that targeted interventions on the most connected reefs in the Reef network, assuming local benefits will spread more efficiently through larval dispersal, including strategies that consider reef state composed of both corals and their main predator (crown-of-thorns starfish). We note that further intervention efficiency and efficacy might be enhanced in the RRAP R&D Program via spatial prioritisation methods and strategy optimisation.

4. METHODS

4.1 Overarching modelling approach

The Great Barrier Reef is a linked social-ecological system influenced by multiple natural and anthropogenic pressures (Bohensky et al. 2011; Anthony et al. 2015; Wolff et al. 2018a). In this project we capture some of the main causal linkages between environmental stressors and ecological responses in space and time. More importantly, we examine how management interventions (new and conventional) can alleviate stress and give Great Barrier Reef corals the best chance of staying resilient under climate change. Our approach to modelling the Great Barrier Reef as a social-ecological system is consistent with the drivers-pressures-state-impact-response framework used in the Reef 2050 Plan and Reef Integrated Monitoring, Modelling and Reporting Program (Figure 1). This chain (or network) of causal links is reflected in the integrated supply chain of models used in this project (see Table 1):

- Ocean warming was informed by climate model projections for the Reef (HadGem2, Wolff et al. 2018), which in turn was informed by Representative Concentration Pathways (RCPs) adopted by the Intergovernmental Panel on Climate Change (IPCC 2014).
- Impacts of storms on flooding, catchment run-off and downstream water quality was estimated from outputs of the coupled hydrodynamic-biogeochemical eReefs model (Herzfeld et al. 2016) and related studies (e.g. Wolff et al. 2018c).
- Physical impacts of storms on the likelihood of coral damage was estimated using a combination of analyses of historical damage and cyclone risk maps under climate change (Puotinen 2007; De'ath et al. 2012; Puotinen et al. 2016; Wolff et al. 2016).

Ocean acidification is a significant and growing pressure on coral reefs globally (Hoegh-Guldberg et al. 2007; Doney et al. 2009; Albright et al. 2016; Anthony 2016a; Gattuso et al. 2018). However, there is high spatial and temporal uncertainty around how ocean acidification will play out on the Reef over coming decades (Anthony et al. 2013; Albright et al. 2016; Mongin et al. 2016), and therefore ocean acidification was not included in this modelling study. We note therefore that projections of coral condition for the no-RRAP scenario (counterfactuals) may be optimistic, especially in a high-CO_2 future (e.g. business as usual: RCP 8.5).

Biological and ecological responses of key coral groups to environmental pressures and management interventions were modelled by two ecosystem models resolved at different spatial scales (see below): CoCoNet (Condie et al. 2018) and ReefMod (Mumby et al. 2007). While the two models are fundamentally different in the way coral population dynamics are represented, they are both able to simulate realistic changes in coral cover across time and space in response to environmental drivers (Figure 1). RRAP interventions were linked to either environmental, biological (e.g. genetic and/or physiological), and/or ecological processes informed by literature or new research. The rationale for using two different ecological models is to provide a fair assessment of RRAP interventions that is not overly influenced by methodological choices, nor by preconceptions about the relative importance of mechanisms driving coral cover across the Reef. This also gives opportunity for robust interventions to emerge, i.e. interventions whose benefits are consistent across models, and ideally across climate change scenarios. By offering different representations of coral demographics, the two models are integral to the simulated counterfactuals as each counterfactual must be seen as a possible scenario of change given the model used.

Resulting patterns of coral condition in space and time for all interventions analyses were made available for the RRAP Concept Feasibility Study values and cost-benefit analyses. The supply chain of models used, and analyses conducted in the project and how they are linked to other sub projects are outlined in Figure 2.

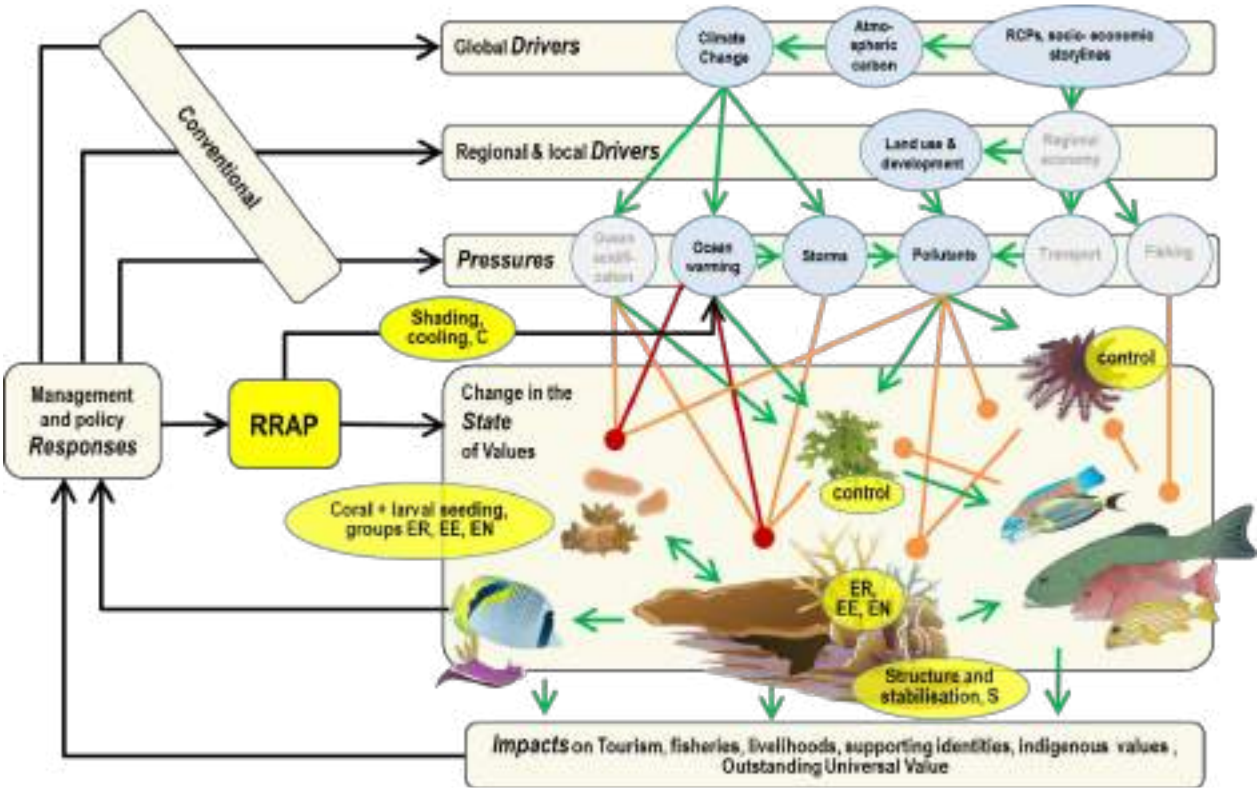


Figure 1: Driver-pressure-state-impact-response (DPSIR) framework used to provide the high-level architecture for the modelling project. Green arrows indicate positive causal relationships and red/orange arrows indicate negative causal ones. While conventional interventions mostly target drivers or pressures, RRAP interventions impact species or other ecosystem components (except cooling/shading which targets a pressure). Ocean acidification is shaded out because it was excluded from consideration in this feasibility study. Similarly, regional socio-economic drivers, fishing and transport were excluded. See **T3—Intervention Technical Summary** and **R2—Intervention Summary** for details of intervention groups. Source: adapted from Anthony (2016a).

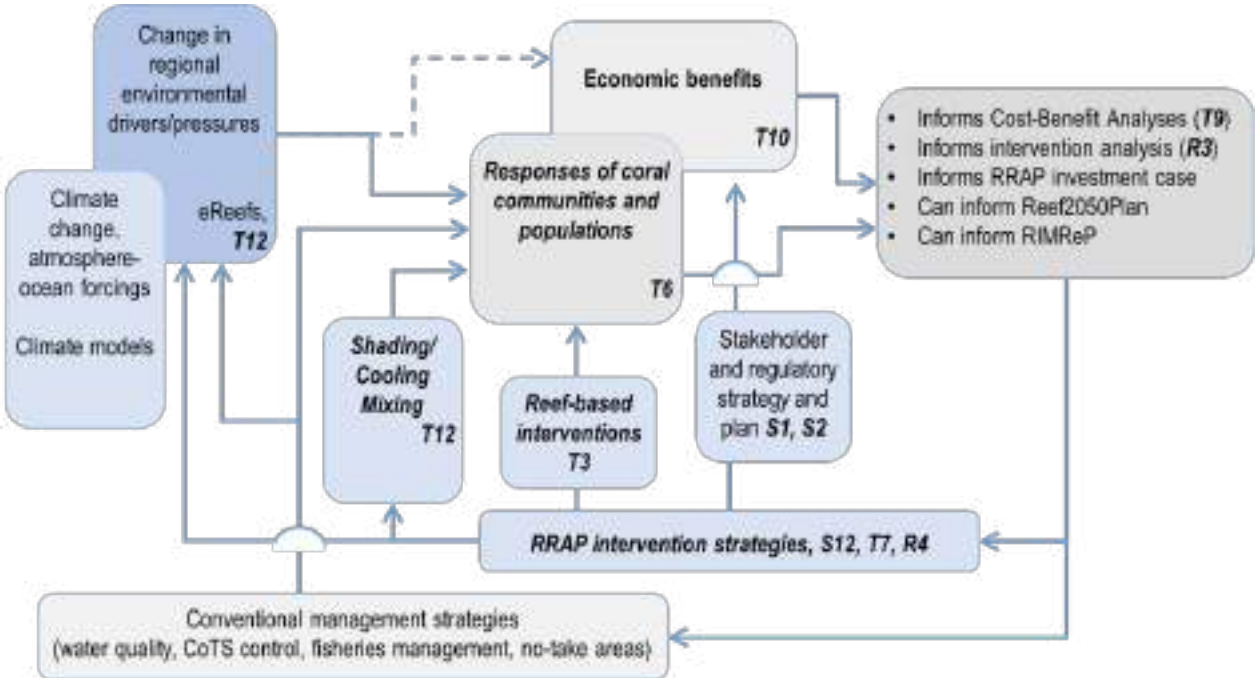


Figure 2: Supply chain of models used in this and linked projects. The models map against the drivers-pressures-state-impact-response framework (Figure 1) in a flow from left to right. As several iterations of the modelling were performed under the RRAP feasibility study, the supply chain was used as an adaptive management framework to test and improve models sequentially within the project.

The following summarises how the different components of the system were modelled and integrated both for the counterfactual and for different intervention strategies (Figures 1 and 2). We keep this summary at a high level and refer to more detailed technical information for each model in the Appendices B1 and B2.

4.2 Environmental forcing: drivers and pressures

The Great Barrier Reef is subjected to a suite of environmental stressors, including cyclones (Wolff et al. 2016; Cheal et al. 2017), associated flooding and run-off of nutrients and sediment (Brodie et al. 2017), heat waves (King et al. 2017) and ocean acidification (Albright et al. 2016). These stressors are likely to interact under climate change such that differing outcomes for the Reef, the broader environment and people are expected for different climate change trajectories (Anthony 2016b; Roth et al. 2017). Projections of global climate trajectories and associated impacts of other environmental pressures are associated with high uncertainty in space and time (Knutti et al. 2005; Bohensky et al. 2011; Thornton et al. 2014; Wolff et al. 2018a). In this project we accounted for environmental and ecological uncertainty, in part by using an ensemble (Monte Carlo) approach by which the ecological models sample randomly from within distributions of parameter values in repeated simulations. We note, however, that this model uncertainty represents only a subset of the real uncertainty in the linked social-ecological system, including deep uncertainties associated with rare events and climate change surprises (Trenberth et al. 2015) as well as our understanding of the network of processes playing out in complex social-ecological systems (Game et al. 2014; Rosa et al. 2017). We represented uncertainty in intervention parameters by formulating conditions representative of pessimistic through to optimistic assumptions of efficacy to explore the envelope of potential benefits. These assumptions are described in more detail for each intervention and climate scenario below.

We used the coupled hydrodynamic-biogeochemical model developed within the eReefs project to drive hydrodynamics and patterns of connectivity between and within reefs. While some changes in future connectivity patterns might be expected, we assume these largely fall within the underlying stochastic variability inherent in the model's specification of connectivity. Currents from eReefs were used to estimate mixing and residence times around individual reefs to understand the feasibility and efficacy of interventions such as: ultra-thin surface films, pumping of cooler water from depth (see **T12—Cool Water Injection and T13—Ultra Thin Surface Films**), and solar radiation management to increase atmospheric reflectance (**T14—Environmental Modelling of Large-scale Solar Radiation Management**). They were also used as the basis for estimating reef connectivity within the ecosystem models. Annual reef connectivity statistics (based on less than a decade of eReefs outputs) were either randomly sampled for each year of simulation (ReefMod) or combined into a statistical distribution that was then used to generate synthetic connectivity patterns each year (CoCoNet). These choices reflect the different structures and computational speed requirements of the two models.

4.2.1 Warming driving coral bleaching

Warming events (thermal anomalies) were modelled as stochastic events informed by historical spatial patterns of heat exposure, expressed as degree heating weeks. In ReefMod, forward projections of sea surface temperature and thermal stress were derived from the UK Hadley Centre Global Environmental Model HadGEM2-ES following RCP 2.6 and 8.5. The coarse (1×1° resolution) Hadgem RCP sea surface temperature trajectories were adjusted to every reef, based on the difference between past Hadisst (1×1°) and CoRTAD (4×4 km) climatology (Wolff et al. 2015, 2018a). Consistent with specification of all forcing in CoCoNet (Table 1), degree heating week projections for RCP 2.6 and RCP 8.5 were specified by analytical functions based on estimates (Wolff et al. 2015, 2018a) and extrapolations of past bleaching events of Lough et al. (2018) (Appendix B1).

Acute summer warming, expressed as degree heating weeks, was used as the principal driver of coral bleaching in both CoCoNet and ReefMod (see below). Chronic warming outside of the summer period was accounted for in ReefMod but not directly in CoCoNet (see Appendix B1 for details). Also, light is a key co-factor in the coral bleaching response (Lesser and Farrell 2004), but was not considered in the models. This may underestimate bleaching likelihood and severity (Skirving et al. 2018) unless warming is already underway (Mumby et al. 2001). The implication is that the efficacy of large-scale solar radiation management (providing both cooling and shading) in lowering coral bleaching risk and mortality could be underestimated here. We emphasise, however, that to understand the real net benefits of cooling and shading on the Great Barrier Reef, as a measure to manage coral bleaching risk, will require full understanding also of all associated risks (see **T14—Environmental Modelling of Large-scale Solar Radiation Management**).

4.2.2 Storms

Tropical cyclones were modelled by CoCoNet as stochastic events with frequencies and intensities consistent with recent historical data (Condie et al. 2018) and relatively uncertain future projections (Cheal et al. 2017). Coral mortality within the spatial footprint of cyclones increased with the category of cyclone (1-5), with a commensurate increase in coral rubble cover (in both models). Cyclone-induced flooding also reduced coral growth rates and increased rates of crown-of-thorns starfish recruitment, again consistent with observations (Puotinen 2007;

Puotinen et al. 2016; Wolff et al. 2016). Coral mortality associated with different categories of cyclones were parameterised using results from post-cyclone surveys (Fabricius et al. 2008). Again, these were applied stochastically to capture the spatial variability in mortality that is typically observed.

In ReefMod, forward projections of cyclone exposure were based on recent (1970–2011) cyclone tracks following the methodology developed by Wolff et al. (2016). These use thousands of simulated cyclone tracks from Kerry Emmanuel (MIT) yet with the frequency and temporal clustering calculated from the historical record.

4.2.3 Water quality

In CoCoNet, a geographical probability distribution for flood plume effects was estimated from the results of available eReefs simulations, with average impacts increasing with proximity to the coast and levels of historical catchment disturbance. Within any year, impacts were distributed stochastically among reefs and increased with storm intensity. Impacts included reduced coral growth and an increase in the survival and recruitment of crown-of-thorns starfish larvae. In ReefMod, forward projections of reef water quality were obtained by repeating the 2011–2016 regime of suspended sediments estimated by eReefs, which affect coral reproduction, recruit survival and juvenile growth.

4.3 Biological and ecological response models: state and state changes

4.3.1 Overview

We used two ecosystem models that resolve two overlapping spatial scales, but at different ecological resolution:

1. CoCoNet (CSIRO): reef level to entire Great Barrier Reef.
2. ReefMod (UQ): from genes to subsections of the Great Barrier Reef.

Here we provide a brief overview of these two models, with more detailed descriptions available in Appendices B1 and B2.

CoCoNet and ReefMod are both spatially explicit models that use environmental drivers and pressures to inform biological and ecological processes that drive the dynamics of reef corals. This includes all processes outlined in Figure 1. By using two models with strengths at different spatial scales and ecological/biological resolution we were better able to establish trajectories under the no-RRAP case (counterfactuals) and to explore the efficacy as well as limitations of interventions operating at different scales.

We use CoCoNet as the main model informing the economic analyses because it covered the entire Reef domain when the modelling integration started in the concept feasibility study. While ReefMod was initially developed for the Cairns region, the model has since achieved capacity to simulate the entire Reef. Also, while both models resolve reef connectivity for both corals and crown-of-thorns starfish (Figure 3, Hock et al. 2014, 2017), CoCoNet explicitly models the control of crown-of-thorns starfish, which has been a major historical driver of coral mortality on the Reef (De'ath et al. 2012; Condie et al. 2018). This makes CoCoNet an effective model for analysing the scope of interventions that have regional to whole-of-Reef scope, specifically: regional-scale solar radiation management and crown-of-thorns starfish control. However, as CoCoNet does not simulate individual corals explicitly (Table 1), it is less suited to the modelling of spatial strategies for the distribution of warm-adapted corals in the Reef network. We note that this caveat should be considered when interpreting results of this intervention.

In addition to CoCoNet we used ReefMod's colony-level resolution and the recently implemented genetics of thermal adaptation as a basis for examining the potential for natural adaptation (in collaboration with Mikhael Matz, University of Texas and Cynthia Riginos, University of Queensland). Adaptation was then emulated within CoCoNet at the whole-of-Reef scale using a much simpler formulation (Appendix B1). By simulating the effect of sea surface temperature on coral growth and reproduction as a heritable trait, ReefMod offers the possibility to track the performance of induced thermal tolerance across generations. Because ReefMod models coral at the individual (colony) level, it is particularly suitable to simulate the fate of outplanted corals and estimate the benefits of a specific amount of coral outplants. ReefMod was also used to resolve interventions that operate at a finer (within-reef) scale, including rubble stabilisation. All ReefMod simulations were run with a focus on the Cairns management area which benefits from recent high-resolution habitat mapping (C. Roelfsema, The University of Queensland). The key characteristics of the two ecosystem models are summarised below in Table 1.

Table 1: Overview of the key components, characteristics and assumptions of the two ecosystem models used in the study

Category	Component	CoCoNet	ReefMod
Model structure and demographics	Geographical coverage	Great Barrier Reef (2096 largest reefs)	Cairns region (156 reefs)
	Resolution (agent)	Individual reef	Coral patch on individual reef
	Coral population structure	Two functional groups: fast- and slow-growing	Six functional groups: arborescent, plating, corymbose/small branching acroporids, pocilloporids, small massive/encrusting, large massives
	Crown-of-thorns starfish population structure	Age structured: larvae (year 0) juveniles (year 1) adults (year 2+)	Age structured: larvae (year 0) recruits (year 0.5) juveniles (year 1) juveniles (year 1.5) sub-adult (year 2) sub-adult (year 2.5) adults (year 3 to 8)
	Reef population connectivity	Connectivity matrices computed from particle-tracking using all available eReefs hydrodynamics (1km resolution) and coral and crown-of-thorns starfish larval behaviour. Statistical probability distributions for connectivity were estimated from these matrices, which were used to distribute reef network connections each simulation year.	Connectivity matrices computed from particle-tracking and eReefs hydrodynamics (4km resolution) including coral and crown-of-thorns starfish larval behaviours. For each simulation year, matrices were randomly sampled from the available eReefs output years.
	Coral rubble dynamics	Coral mortality generated rubble that inhibited coral larval recruitment.	Coral mortality generated rubble that decreased the survival of coral juveniles.

Category	Component	CoCoNet	ReefMod
	Natural thermal adaptation in corals	Surviving a bleaching event enhances thermal tolerance. Trait passed on to next generation (reef-scale means limited the propagation of extreme traits). Assumes no negative effects (trade-offs) of being 'warm adapted' during cooler periods.	Polygenic model of coral's optimum temperature driving fitness to chronic warming and resistance to acute thermal stress. Growth performance and breeding determined by current temperature relative to corals' thermal optimums; resistance to bleaching dependent on thermal optimums. Genetic quantitative traits passed to next generation with varying levels of heritability.
Environmental impacts	Tropical cyclones	Coral mortality was dependent on coral type and storm/cyclone intensity. Past: random events applied at frequencies and intensities consistent with historical conditions. Future: 50 percent higher frequency of category 5.	Coral mortality was dependent on coral type and cyclone intensity. Past: spatially explicit historical time-series of events were applied. Future: time-series of events using synthetic cyclone tracks based on historical frequencies and temporal clustering. Assumes cyclone intensity does not change under climate change*.
	Flood plumes	Storm-induced flooding reduced coral growth rates and increased rates of crown-of-thorns starfish recruitment. Effects increased with storm intensity, proximity to the coast and historical catchment disturbance. See details of assumptions in Appendix B1.	Water quality determined by eReefs sediment transport (4km resolution). Suspended sediment reduced coral reproduction, recruitment and juvenile growth rates. Past: 2011–2016 hydrologic regime, including summer flood plumes. Future: 2011–2016 regime repeated in cycles.
	Coral bleaching	Bleaching-related mortality depends on coral type and degree heating weeks. Past: frequencies and intensities consistent with historical records. Future: increased frequency and intensity of events consistent with climate projections.	Coral mortality depends on coral type and degree heating weeks following recent observations of bleaching-induced mortalities on the Reef from Hughes et al. (2018). Past: spatially explicit historical time-series of events. Future: increasing frequency and intensity of events consistent with climate projections.
Interventions	Catchment restoration	The influence of floods on coral growth and recruitment of crown-of-thorns starfish larvae was reduced over a specified time scale.	Not modelled
	Crown-of-thorns starfish control	A fleet of control vessels (each operating 25 x 10 voyages per annum) targeted reefs with high adult crown-of-thorns starfish populations, with additional priority given to highly connected reefs. Cull was limited by the detectability of crown-of-thorns starfish.	Used CoCoNet predictions of crown-of-thorns starfish densities
	Rubble stabilisation	A specified area of rubble was stabilised targeting reefs with extensive rubble and low coral cover. Highly connected reefs prioritised.	A specified area of rubble was stabilised targeting reefs with extensive rubble. Highly connected reefs prioritised in the Cairns region.
	Solar radiation management	A uniform reduction in degree heating weeks specified for the Reef.	Reduction in degree heating weeks relative to coral's optimum temperatures in the Cairns region

Category	Component	CoCoNet	ReefMod
	Introduction of thermally tolerant corals	Simulated outplanting of a specified area of thermally tolerant coral. Targeted reefs with low coral cover, with additional priority given to highly connected reefs.	Explicit outplanting of individual corals on the reef surface. Coral juveniles (2cm) deployed with artificially enhanced optimum temperatures (+1°C, +2°C). Targeted simulated outplanting on reefs with low coral cover in the Cairns region, with additional priority given to highly connected reefs.

* This is consistent with the output of some of the cyclone models for the region, but we note that there is considerable disagreement among the entire ensemble of models as to the frequency and intensity of future cyclone events in the region.

4.4 Details of the reef ecosystem models

4.4.1 CoCoNet: Great Barrier Reef-scale community model

The Coral and CoTS Network (CoCoNet) meta-community model was developed by Condie et al. (2018) (Figure 3, Appendix B1). It models coral and crown-of-thorns starfish dynamics using individual coral reefs as agents. CoCoNet was calibrated against data from the Australian Institute of Marine Sciences (AIMS) Long-term Monitoring Program. In essence, CoCoNet consists of a dynamic network of individual reefs connected through larval recruitment of corals and crown-of-thorns starfish. The most recent implementation uses a network of 2096 reefs, corresponding to size and location of the largest reefs within the Great Barrier Reef (the Reef). A technical description of CoCoNet implemented on a smaller reef network is presented in Condie et al. (2018a).

CoCoNet models meta-populations of fast-growing corals (e.g. *Acropora* and *Montipora* spp.) and massive slow-growing corals (e.g. Faviidae and *Porites* spp.); as well as age-structured populations of crown-of-thorns starfish, the major coral predator on the Reef. Trophic interactions in CoCoNet are determined using a model that includes feeding preference for fast-growing coral and rate parameters (growth, predation and natural mortalities) fitted to data from the AIMS Long-term Monitoring Program (Morello et al. 2014). Each reef has a fixed coral-carrying capacity proportional to the area of the reef.

Reef connectivity, involving spawning, larval transport by ocean currents and successful settlement onto either a natal reef (self-recruitment) or neighbouring reefs (cross-recruitment), was modelled as directed links that appeared and disappeared from year to year with exchanges that also varied stochastically to represent variability in ocean currents and larval survival. The probability of successful recruitment from one reef to another was proportional to the connectivity estimated from particle tracking experiments using ocean currents from the eReefs hydrodynamic model (Hock et al. 2014, 2016, 2017; Condie and Condie 2016). However, recruitment levels were reduced by the presence of coral rubble generated by coral mortality during cyclone and bleaching events. As part of the calibration process, recruitment probabilities were also weighted for each coral and crown-of-thorns starfish group to align the modelled median and range of coral and crown-of-thorns populations with observations from the AIMS Long-term Monitoring Program.

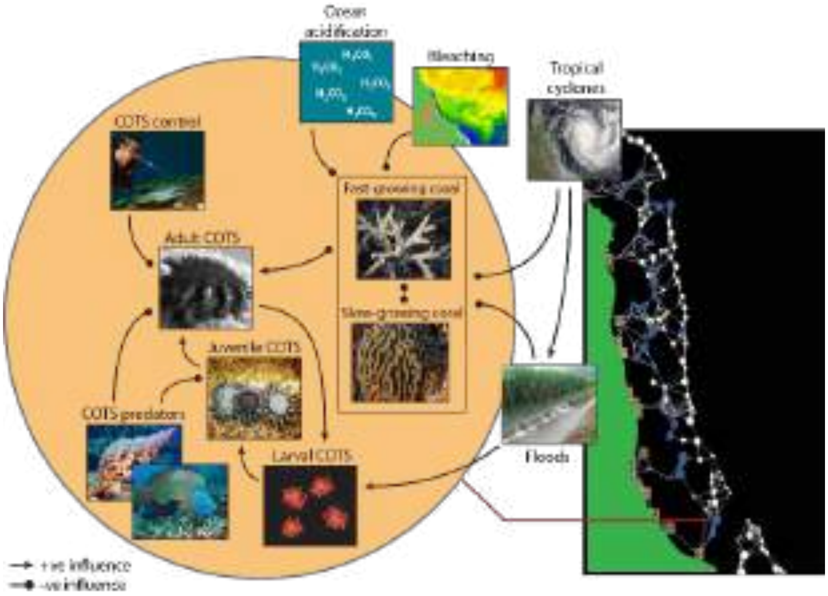


Figure 3: Conceptual layout of the Coral and CoTS Network model (CoCoNet). CoCoNet is characterised as a minimum realistic model using broad coral functional ecological groups. It uses age structures for crown-of-thorns starfish (COTS) and resolves recruitment for corals and crown-of-thorns starfish across 2096 reefs. CoCoNet uses stochastic environmental forcing and is calibrated against (or aligned with) monitoring observations at multiple spatial and temporal scales, including using the AIMS Long-term Monitoring Program data. Source: modified from Condie et al. (2018).

4.4.2 ReefMod-GBR: modelling fine-scale ecological processes

ReefMod simulates individual coral colonies interacting in a two-dimensional reef space (Mumby et al. 2007; Ortiz et al. 2014; Bozec et al. 2015). In essence, the model grows coral reefs in a virtual, simulated environment using the principle of agent- or individual-based modelling. Space is represented by a grid lattice of 20×20 cells, each approximating 1m^2 of the reef floor (Figure 4, Appendix B2). Each grid cell can be occupied by multiple coral colonies of different species. The model integrates physiological, population-level and community-level processes for benthic reef assemblages in space and time using dynamic environmental exposure layers (past, present or future) as input. For the present application, we extended a previous model parameterisation developed for an isolated Pacific reef system (Ortiz et al. 2014) allowing the simulation of six characteristic morphological groups of *Acropora* (tabulate, arborescent, corymbose) and non-*Acropora* corals (corymbose, small massive and encrusting, large massive corals). A focus on *Acropora* corals is justified as they represent the key habitat-forming species on Indo-Pacific reefs and account for around 70 percent of the coral biodiversity in the region (Wallace 1999).

A regional model for the Great Barrier Reef (ReefMod-GBR) was developed by assigning a 20×20 grid lattice to each of 3806 individual reefs of the region (see details in Appendix B2). Because environmental forcing (environmental cause-and-effect relationships) and habitat classification is not consistently available at intra-reef scales (<1km), a reef is considered here as a homogeneous environment and is therefore represented by a 20m×20m space. The 3806 reef populations are connected by larval dispersal (Hock et al. 2017) and exposed to dynamic layers of water quality, cyclones and thermal stress that are representative of the physical environments of the Reef (Figure 4). In addition, the model was augmented with explicit mechanisms driving the early life-history stages of corals: coral reproduction, coral settlement, and growth and mortality of coral recruits. A new parameterisation of coral recruitment, growth and mortality (including bleaching mortality) was developed based on recent empirical data from the Reef. For RRAP, we implemented natural processes of rubble formation and stabilisation which affect coral juvenile demographics. In addition, an explicit model of crown-of-thorns starfish population dynamics was integrated allowing to simulate the impacts of crown-of-thorns starfish outbreaks on coral populations (Figure 5). Finally, a quantitative genetic model of thermal tolerance was integrated following the model of Matz et al. (2018), allowing the model to account for thermal adaptation in projecting future coral condition.

Specifically, for RRAP, ReefMod-GBR was configured to simulate interventions in the Cairns region only, where recent high-resolution habitat mapping (C. Roelfsema, The University of Queensland) provides the most accurate estimates of reef area at depth 3-10m (a depth range representative of the demographic parameters used in ReefMod). Accuracy in the existing amount of reef habitat is key for measuring restoration effort associated with several interventions (e.g. quantities of outplanted corals, amount of stabilised rubble). It is anticipated that high-resolution habitat mapping will become available for the entire Reef during the RRAP R&D Program, so the benefits of intervention will be assessed for the 3806 reefs of ReefMod-GBR.

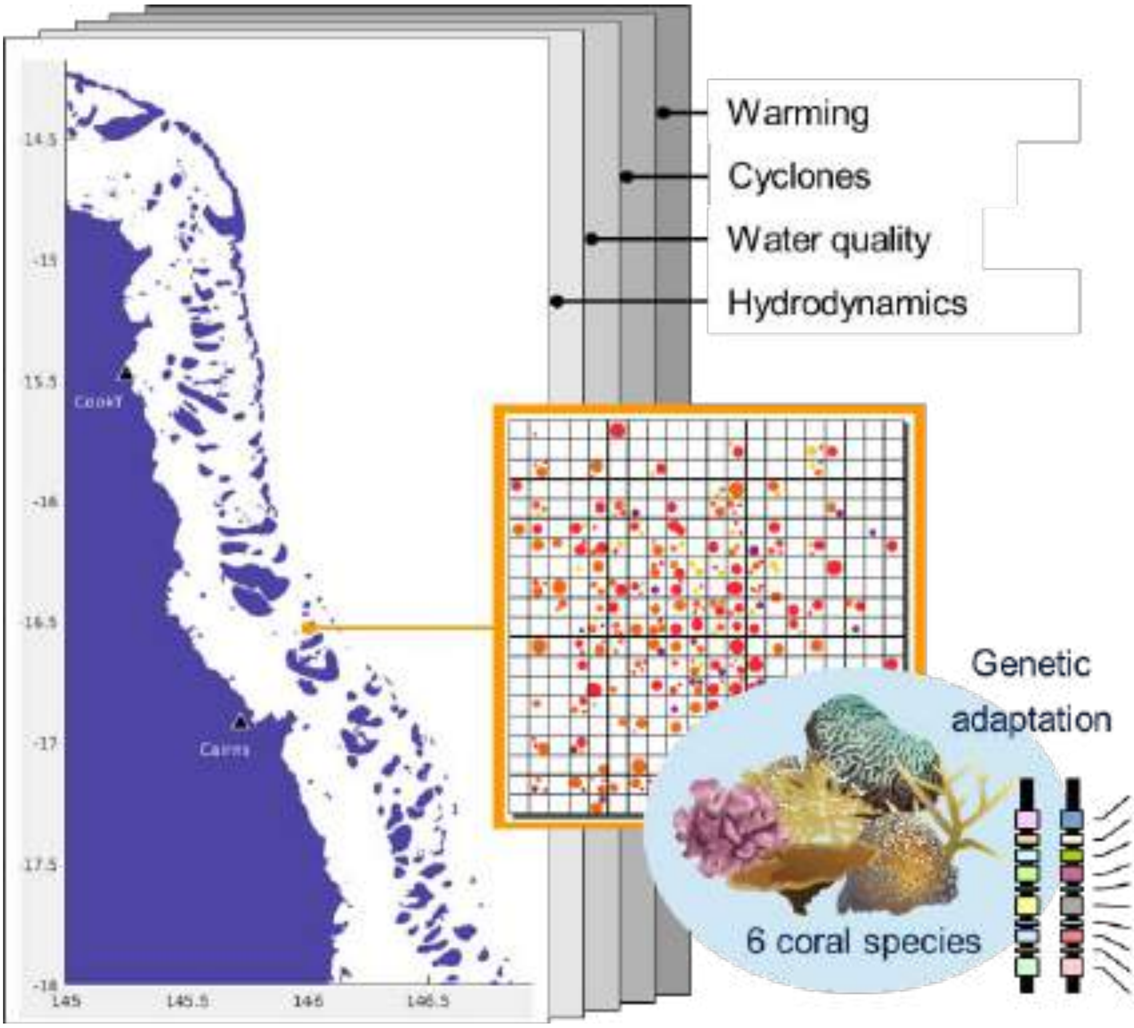


Figure 4: Schematic representation of ReefMod-GBR (Bozec, Mumby, UQ) with a focus on the Cairns management area for RRAP. Individual coral colonies are typified by circular areas of variable size. Corals settle, grow, shrink and die in a virtual 20m×20m environment as they do in situ. Demographic rates are specific to the six modelled coral groups. Similar to CoCoNet, demographic rates and connectivity are forced by environmental variables in space and time. Because ReefMod-GBR resolves fitness components for individual coral colonies driven by genes, it was used to

examine the role of natural adaptation of corals under climate change. See also Figure 5 and Appendix B2. Graphics: IAN image library and YM Bozec.

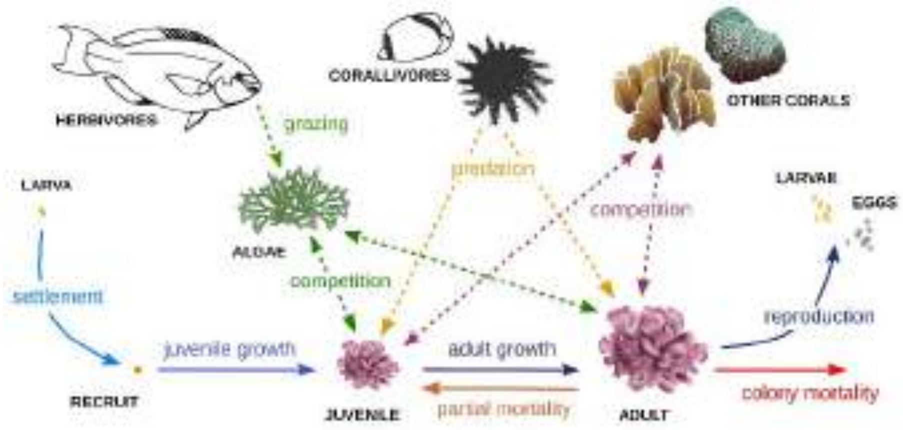


Figure 5: Demographic processes (solid arrows) and ecological interactions (dashed arrows) affecting corals in ReefMod. Processes are spatially explicit and occur across a 20m×20m reef surface at the level of coral individuals (individual-based model, see also Figure 4 and Appendix B2). Graphics: IAN image library and YM Bozec.

4.5 Modelling impacts of drivers and pressures

4.5.1 Coral bleaching and associated mortality

Coral bleaching risk was modelled probabilistically based on the annual likelihood of accumulating heat stress (expressed as degree heating weeks) above the local maximum monthly mean (Eakin et al. 2009). In CoCoNet, bleaching risk was simulated to increase through time at rates dependent on the RCP scenarios (Lough et al. 2018), whereas ReefMod used spatial projections of maximum degree heating weeks from climate models (Wolff et al. 2018a). In both models, coral mortality associated with mass bleaching was projected from empirical observations between coral mortality and degree heating weeks based on data from the 2016 mass bleaching event on the Reef (Figure 6, Hughes et al. 2018). In CoCoNet, a Gompertz function (Figure 6) was fitted to observations of the amount of bleaching mortality observed in 2016 (Hughes et al. 2018) while Reefmod directly modelled coral colony mortality as a function of degree heating weeks based on data from Hughes et al. (2018). See Appendix B1 and B2 for details. To predict bleaching-related coral mortality associated with heat stress in a given year in simulations, degree heating weeks used as an input were drawn randomly from either beneath the squared maximum degree heating weeks forecasts (CoCoNet) or from degree heating weeks produced by outputs from a climate model (ReefMod).

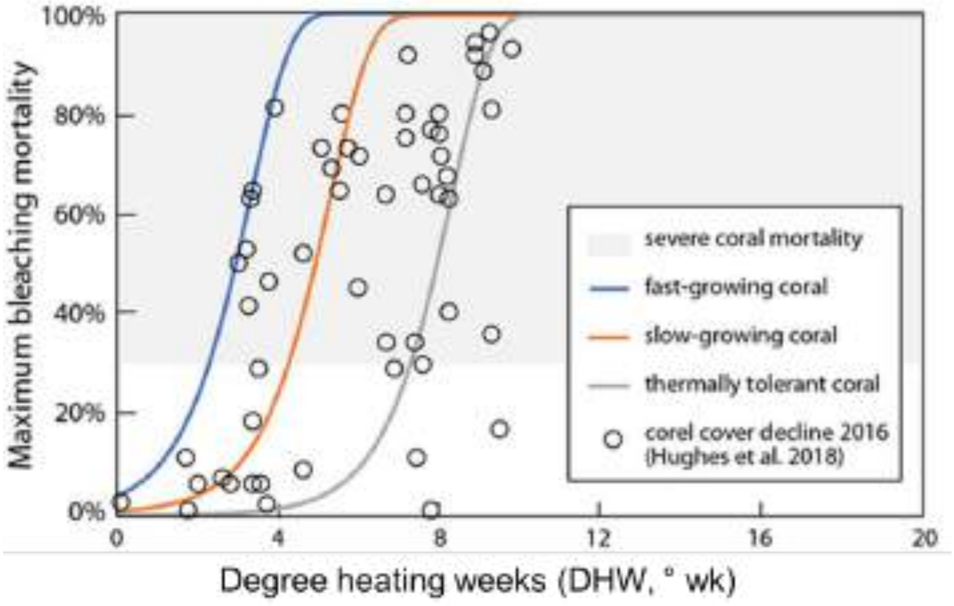


Figure 6: Bleaching severity as a function of cumulative summer heating fast-growing and slow-growing coral groups used in CoCoNet, as well as thermally tolerant coral introduced only in specific scenarios. Bleaching severity was used as a proxy for bleaching mortality in CoCoNet. Data points are observed bleaching severities on individual reefs following the 2016 bleaching event on the Reef (Hughes et al. 2018).

4.5.2 Performance metrics: coral cover and condition

Ecological modelling in this project focused on the cover of reef-building corals for three main reasons. First, reef-building corals are the primary habitat-forming structures on tropical coral reefs, supporting the richest diversity in the ocean (Fisher et al. 2015). Without corals, the Reef would lose its fine-scale three-dimensional structure that provides habitat for more than 120,000 macroscopic species of fish and invertebrates (GBRMPA 2013). Disturbances that lead to severe loss of three-dimensional reef structure can lead to dramatic decline in major groups of reef fishes: 40-65 percent for predatory fishes (e.g. coral trout and emperors), up to 65 percent in wrasses and 90 percent for butterfly fishes (Emslie et al. 2014). Conversely, preserving complex fish habitat by sustaining three-dimensional coral cover can help sustain scope for a diverse reef fish community. Second, many ecosystem services on coral reefs can be linked to coral condition. For example tourism value is in part linked to coral condition aesthetically (Vercelloni et al. 2018) and fisheries value is linked to the quality and quantity of habitats for young and adult fish and their prey (Rogers et al. 2014). Further, the capacity of a coral reef to offer coastal protection under climate change scales with its capacity to maintain and grow structure in pace with sea level rise and physical damage (e.g. Woesik et al. 2015). Finally, around 400 species of reef-building corals are found on the Reef, thereby representing significant biodiversity in themselves (Wallace 1999; Veron 2000).

We use two metrics to describe coral condition: (1) coral cover and (2) a simplified Reef Condition Index (RCI). Coral cover is the standard metric used to describe coral abundance (De'ath et al. 2012; Richards 2013). However, coral cover provides limited information about the quality of the coral real estate, and therefore provides limited insight into consequences for ecosystem values and services. For the purpose of the economic analyses we use the simplified RCI, which captures the contribution from branching, fast-growing coral groups relative to total coral cover. Ideally, RCI should also account for 3-dimensional structural complexity to provide insight into habitat provision for fish and invertebrates, but this was out of scope for CoCoNet in this study. We define RCI here as the product of (1) a subindex for coral cover and (2) a subindex for composition (fast versus slow-growing corals). The two subindices are non-dimensional and range from 0 to 1 (Figure 7). For simplicity we set intercepts in Figure 7 (Icov base, Icomp_base) to 0 and thresholds for when RCI = 1 (cov_thr and comp_thr) to 50 percent. The rationale for using this threshold is that most ecosystem services will be most sensitive to changes in coral cover and composition below 50 percent.

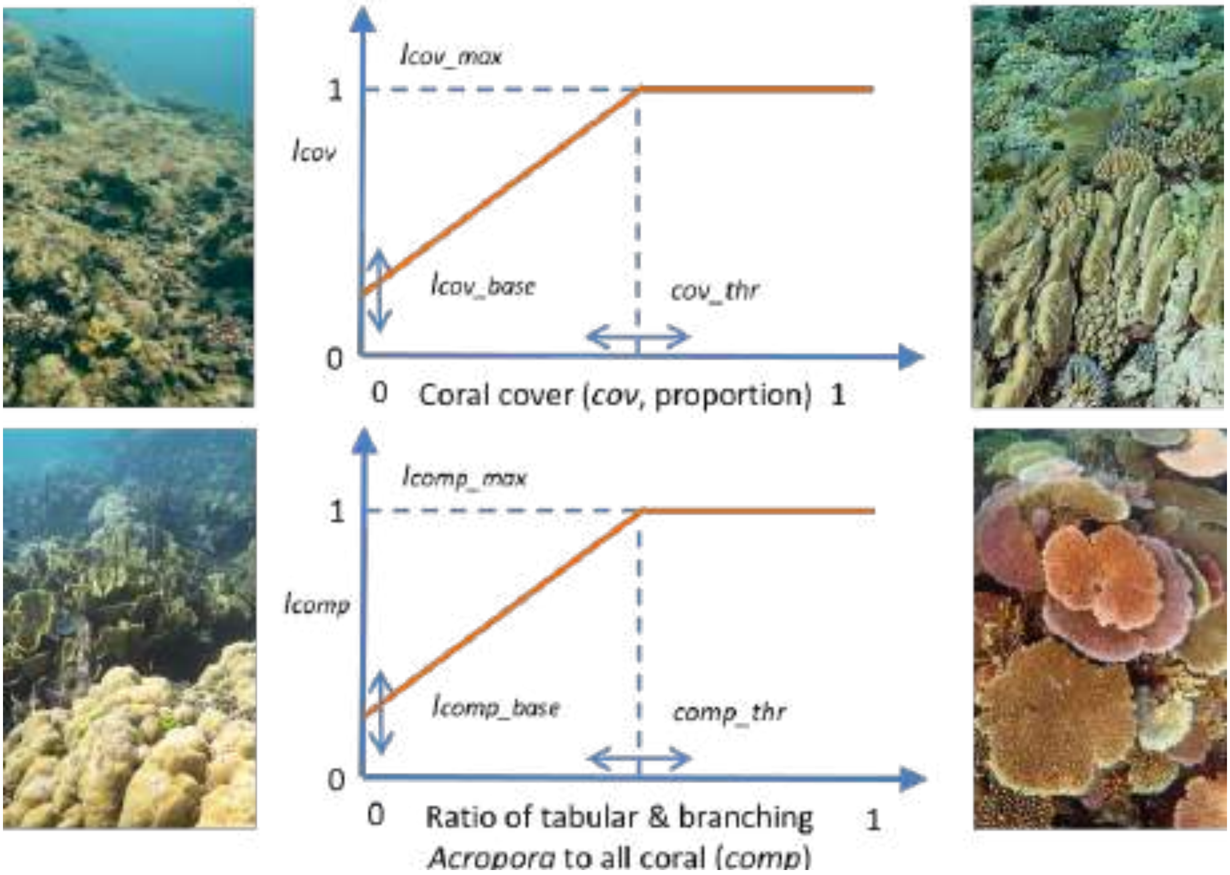


Figure 7: Two subindices used to estimate Reef Condition Index (RCI) as a complement to coral cover. A simplified RCI (as RCI = Icov * Icomp) was used as a metric for the analysis of benefit streams, and subsequently the cost-benefit analyses, because RCI facilitated better translation to ecosystem services such as tourism, fisheries, existence values and supporting identities than coral cover alone.

4.5.3 Natural adaptation of corals to thermal stress

ReefMod

ReefMod accounted for the evolutionary dynamics of coral fitness to temperature change by integrating a quantitative genetic model of thermal tolerance and adaptation. Phenotypic tolerance to increasing sea surface temperature was implemented following the polygenic model developed by Matz et al. (2018). Briefly, thermal tolerance of a coral colony was shaped by a set of quantitative trait loci that were transmitted from parents to offspring. Each thermal quantitative trait locus was associated with an effect size (in °C) and the sum of effect sizes over all loci gave the breeding value for thermal tolerance (see Appendix B2). The actual phenotype was obtained by adding a random noise to the breeding value (genotype) to model imperfect heritability. This process sets a specific phenotypic optimum (Topt) to every coral from which thermal fitness was calculated relative to the ambient temperature.

At each time step, thermal fitness was evaluated for each coral by calculating the difference between Topt and the mean annual sea surface temperature of the Reef, with thermal fitness declining away from Topt for warmer and colder temperatures. A reduction in fitness reduced growth and fecundity proportionally. While available experimental evidence is quite limited for a robust parameterisation of the shape of this curve, the simplistic approach is to assume that coral fitness follows a Gaussian curve (Matz et al. 2018) so that change in fitness is symmetrical on the warm and cold sides. An important parameter is the width of the Gaussian curve which reflects the breadth of thermal tolerance (see Appendix B2). While this parameter is likely to vary among species, there is currently no available data to set a specific parametrisation of thermal tolerance for each of the six functional groups. Following Matz et al. (2018), we simply explored two scenarios where fitness dropped by either 39 percent (narrow thermal tolerance) or 13 percent (broad tolerance) when temperature deviates from Topt by ±1°C (see Figure 8, see Appendix B2 for a justification of thermal tolerance bounds).

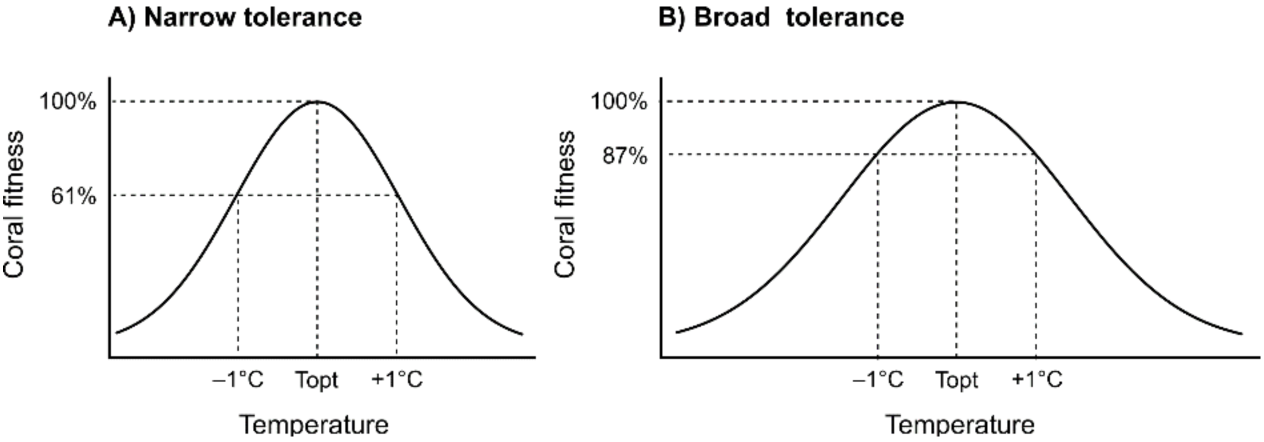


Figure 8: The two scenarios of thermal adaptation. Coral physiological response to temperature is a bell-shaped curve centred on their thermal optimum (Topt) which is determined by their genes. Coral fitness (growth, reproduction) is maximal (100 percent) when temperature perfectly matches the thermal optimum and decreases as temperature moves away. The width of the fitness curve defines the breadth of thermal tolerance, and two scenarios of are considered here whereby a 1°C mismatch between the current temperature and Topt leads to a 39 percent (A) or 13 percent (B) drop in fitness.

The phenotypic expression of thermal tolerance also includes a greater resistance to bleaching and it is assumed that sensitivity to extreme temperatures is proportional to Topt (see details in Appendix B2). While thermal fitness results in the selection of the most tolerant and well-adapted phenotypes to chronic fluctuations in temperature, the success of adaptation to warming is also driven by the efficiency of trait transmission from one coral generation to the next. Following Matz et al. (2018), heritability is represented by the strength of the correlation between Topt and the breeding value. Heritability is perfect when Topt perfectly matches the breeding value; in this case, a chronic increase in temperatures might result in an efficient selection of genes that confer thermal tolerance, leading to a rapid evolution of thermal traits. Conversely, strong deviation between Topt and the breeding value can lead to selecting genes that are not related to the actual fitness of the coral. In this case, the evolution of thermal traits is likely to be slow, although a greater diversity of phenotypes in the population might buffer the selective pressure of increasing temperatures.

CoCoNet

Representation of natural adaptation in CoCoNet was significantly less sophisticated than that used in ReefMod. While including essential processes such as selection during thermal stress events and trait transmission between coral generations, the model formulation was highly simplified with parameters selected to ensure broad consistency with mid-range adaptive responses to modelled sea surface temperature projections (Logan et al. 2014), as well as projections from the ReefMod counterfactuals. Because the CoCoNet adaptation results were not independent of ReefMod, their usefulness was mainly in extrapolating trends to the whole-of-reef scale.

Following each bleaching event, the thermal tolerance of surviving corals (measured in degree heating weeks) was increased, with a proportionate penalty in growth rate (Appendix B1). In the absence of thermal stress, thermal tolerance gradually declined again as the community structure within each coral group recovered (Maynard et al. 2008; Sampayo et al. 2008; Van Woesik et al. 2011) or corals shuffled their zooxanthellae populations to more thermally tolerant symbiont types (Sampayo et al. 2008; Logan et al. 2014). See further details around assumptions in Appendix B1.

Thermal tolerance was assumed heritable in that recruitment from neighbouring reefs contributed to the average thermal tolerance of the receiving reef. However, this averaging at the reef scale would have limited the propagation of traits, except to reefs where existing coral cover was very low. An implicit model assumption is therefore that local adaptation in direct response to heat stress tends to be the main driver of adaptation, rather than propagation of traits from reef to reef.

4.6 Modelling new interventions

This modelling study and subsequent economic analyses explored a set of three example interventions operating at different spatial scales and impacting on different processes in the system (Figure 1). Importantly, the purpose of this set of example interventions was to illustrate the scope that RRAP might have in enhancing coral condition through multiple avenues. We emphasise that these interventions do not represent specific recommendations for further research and development under RRAP or for actual deployment.

The example set of new interventions along with conventional ones are represented conceptually in Figure 9 (see also Figure 1). Here, conventional management interventions are tagged with a green marker (indicating they are in use), with the size of the marker indicating the spatial scale at which the intervention operates. New interventions are marked yellow to red.

4.6.1 Enhanced thermal tolerance of corals

We refer to the first category of interventions as ‘enhanced corals’, which capture the broad set of interventions that can help build enhanced thermal resistance in corals. These include assisted evolution (AE), assisted gene flow (AGF), assisted colonisation (AC) and gene editing (GE) (van Oppen et al. 2015, 2017; Anthony et al. 2017). While none of these interventions are yet field ready (NASEM 2018), as indicated by colour tags in Figure 9, they have varying expected scope to build resilience at scale (indicated by sizes of colour tags, see also Interventions Report – T3). In this modelling study, we explored the effects of enhanced thermal resistance in corals regionally and Reefwide, while being agnostic to the specific intervention mechanism by which such thermal resistance is achieved. Further, we exclusively explore potential benefits of interventions – i.e. we do not formally analyse downside risks in the ‘enhanced corals’ category, such as the introduction of invasive species or pathogens or outbreeding depression (Aitken and Whitlock 2013), or the risk of producing a genotype/phenotype with superior fitness outcompeting other coral species (see T3). We made these simplifying assumptions because risks will vary greatly among methods of building thermal resistance and resilience in corals (see **T3—Intervention Technical Summary, T5—Future Deployment Scenarios and Costing, R3—Intervention Analysis and Recommendations**).

In CoCoNet, enhanced thermal tolerance of corals due to intervention was modelled by simulating the outplanting of corals with a conservative 0.4°C added tolerance. Given 12 weeks in the bleaching season, this corresponds to a right-shift of approximately 5-degree heating weeks on the bleaching mortality/degree heating weeks curve (Figure 6). For ReefMod, this was simulated by enhancing the thermal optimum of deployed corals by 1°C (or 2°C) relative to the native population. The spatial design by which the thermally-tolerant corals were deployed in the simulations was governed by coral connectivity patterns previously established across the entire Reef and informed by eReefs hydrodynamic models (Hock et al. 2014, 2016). Specifically, for Reefwide simulations (CoCoNet), a total of 10 or 100 million warm-adapted corals (corresponding to 2ha or 20ha of added corals) were deployed annually at 100 of the 500 most connected reefs in the Reef network of reefs. Given the simulated deployment started in 2031 and continued until 2075, this amounts to a total of between 90ha and 900ha of new corals over the 45-year time horizon. Both ReefMod and CoCoNet used a deployment algorithm by which only reefs with coral cover lower than 20 percent were targeted annually, considering coral juveniles should be deployed only at depauperate reefs in order to facilitate their recovery.

Because each coral group (fast- versus slow-growing) represented several coral species, interbreeding was limited in CoCoNet to a set proportion of the fast-growing or slow-growing population. Specifically, bleaching-resistant corals were assumed to be capable of interbreeding with 10 percent of the native fast-growing coral group (and 0 percent of the native slow-growing group). Hybrids recruited to each reef were proportionally allocated to each of the two interbreeding groups, with proportionate changes in their bleaching resistance.

In ReefMod, outplanted juvenile corals were assumed to be 2cm in diameter with equal deployment densities of branching *Acropora* and corymbose groups. Different scenarios of coral outplanting were assessed, whereby 20, 40 or 80 million juveniles were seeded on 10 or 20 reefs in the Cairns region. Corals were outplanted at random over each reef grid at two specific densities (0.5 or 1 coral per m^2), targeting the most highly connected source reefs. Outplanted corals were allowed to breed with native corals from the same functional group, thus enabling genes of warm-adapted outplants to be spread across the connectivity network.

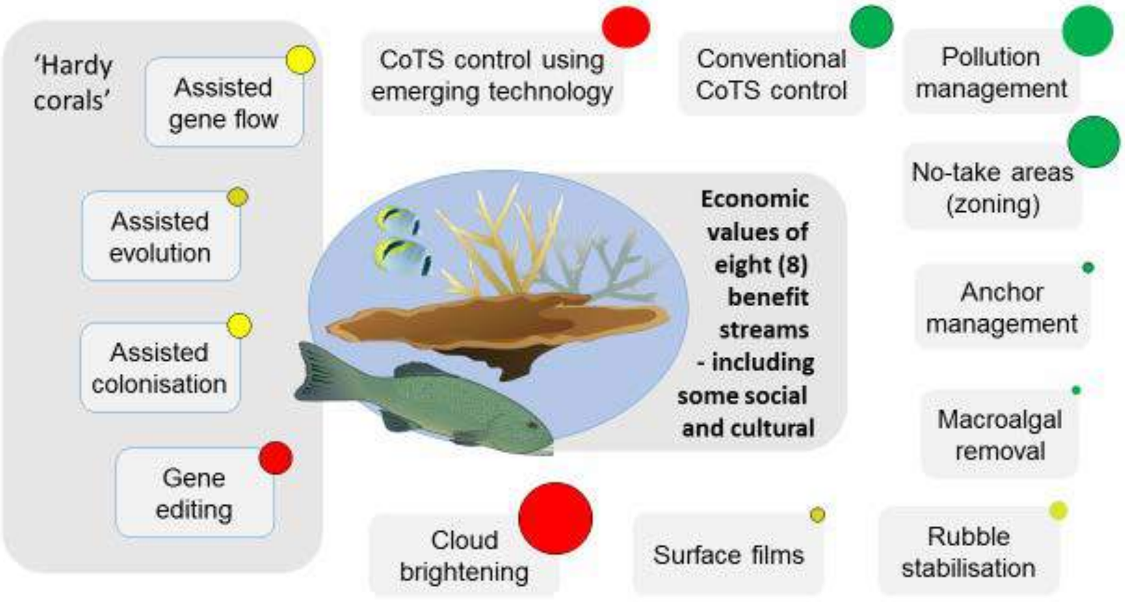


Figure 9: Examples of conventional and emerging interventions on the Reef. In the model analyses of this project, the key conventional management interventions were crown-of-thorns starfish control, pollution management and implicitly no-take areas, the later via model alignment with observations. Model simulations of enhanced thermal tolerance in corals broadly used the category 'enhanced corals', while being agnostic about the technique conferring such thermal tolerance. Further, simulating crown-of-thorns starfish control using emerging technology simply assumed that a new intervention could increase crown-of-thorns starfish mortality to the extent that populations could be suppressed to below outbreak density (Westcott et al. 2016). Key to symbols: size of bubble indicates spatial scale and colours indicate tentative risk or readiness levels (red: not deployment ready, green: ready or already being implemented).

4.6.2 Solar radiation management – large scale

We used cloud brightening as a representative example of large-scale solar radiation management of relevance to RRAP, noting that the results are also applicable to other large-scale solar radiation management interventions. Solar radiation management was modelled as a reduction in the degree heating week stress exposure at regional (ReefMod) or Reefwide (CoCoNet) scales. Based on large-scale albedo assessments, we assumed potential cooling of reef surface waters may fall by between 0.3 to 0.7°C during austral summer (see**T14—Environmental Modelling of Large-scale Solar Radiation Management**). Given 12 weeks in the bleaching season, we assume cooling from solar radiation management could be in the order of ~ 4-8-degree heating weeks.

In addition to cooling, other solar radiation management approaches reduce light stress; specifically, reduction in surface irradiance by large-scale solar radiation management scales with the amount of cooling which could be achieved. Light is a co-factor in the coral bleaching response on photosystem 2 in coral symbionts (Lesser and Farrell 2004, Anthony et al. 2007, Skirving et al. 2018). Conservatively, however, we excluded reduction in light stress from the bleaching response at this time, because the quantitative partitioning of temperature and light influences on bleaching mortality are not yet well characterised (Skirving et al. 2018).

A program of large-scale solar radiation management during the summer months operating continuously over many years naturally raises numerous considerations of potential impacts on the reef ecosystem. This includes a reduction in light-availability for phototrophs in deeper habitats (including meso-photic reefs). Consistent with our modelling of enhanced thermal tolerance, quantitative analysis of unintended impacts of solar radiation management was considered out of scope for this RRAP Concept Feasibility Study. Nevertheless, it is important to note that while large-scale solar radiation management on the Reef conducted over long periods will alleviate coral exposure to heat and light stress (and consequently bleaching risk) it may also slow the rate of adaptation that would have occurred in the absence of solar radiation management. The potential risk is that future accidental failure (or decommissioning) of the solar irradiance management system may lead to more severe bleaching and mortality than if solar radiation management had not been implemented. Importantly, however, large-scale cooling and shading considered in this project involves enriching the lower atmosphere over the Reef with sea salt particles, in effect expanding the natural envelope of salt spray as a management intervention. This is different from aerosol injections in higher strata proposed for geo-engineering projects (Matthews and Caldeira 2007; Barrett et al. 2014). Finally, as this project only assesses the potential benefit of solar radiation management (as reduced degree heating weeks of exposure), we note that any risks associated with reduced adaptation and cooling and shading system failure must be considered in the interpretation of modelling results.

4.6.3 Crown-of-thorns starfish control

The control of crown-of-thorns starfish using conventional, manual means (Rivera-Posada et al. 2012; Pratchett et al. 2014) is growing in intensity on the Reef and is managed and coordinated by the Great Barrier Reef Marine Park Authority. Current and planned crown-of-thorns starfish control efforts for 2019/20 amount to eight control/surveillance vessels operating along the entire Reef (pers comm, D Cameron). While conventional crown-of-thorns starfish management is becoming increasingly effective at protecting individual priority reefs during the current outbreak (D Westcott, pers comm), the scope for containing or arresting a full-scale crown-of-thorns starfish outbreak using conventional means is low, in part due to the low detectability and culling efficacy of juvenile starfish (Walshe and Anthony 2017). Therefore, because crown-of-thorns starfish remain a significant risk to corals on the Reef, and would represent a high risk to investments in thermally-enhanced coral populations, there is an argument for investing in additional high-efficacy crown-of-thorns starfish control that can suppress starfish densities to below the outbreak threshold, referred to here as the No CoTS Outbreaks (NCO) option. Our modelling of this, largely hypothetical, option was agnostic of any technique by which such additional crown-of-thorns starfish control suppresses crown-of-thorns starfish densities to below the outbreak threshold. Therefore, understanding true benefits, risks and costs will require a separate study of specific crown-of-thorns starfish intervention options.

Implementation of conventional crown-of-thorns starfish control at the business-as-usual level in the model aligned with the approach used by control vessels currently operating on the Reef. We acknowledge here that 2-4 vessels are truer of the recent business-as-usual reality, but we model eight vessels as they are likely to represent the situation by 2020. In simulations, each vessel was set to operate 250 days per year, which was divided into 25 ten-day voyages, with a maximum of 90 percent of this time spent on-reef. For each voyage, highly connected reefs and then other reefs were checked at random until a crown-of-thorns starfish outbreak (>0.2 starfish per survey unit, see Appendix B1) was detected. Every time a reef was checked, 0.1 days of the available voyage time was removed to capture the impact of increased transit times when outbreaks were rare.

Further, for the conventional, business-as-usual level of crown-of-thorns starfish intervention (here assuming eight control vessels), once an outbreak was identified, this reef was targeted along with other reefs within a radius of 6-14km (selected randomly). The detectability of adult crown-of-thorns starfish on the Reef was initially estimated to be in the range 77-87 percent (MacNeil et al. 2016). However, recent studies suggest that this figure is optimistic (M. Pratchett, pers com) and a more conservative rate of 60 percent was adopted for CoCoNet simulations. The time each control vessel spends on each reef increased linearly with the area of the reef, with the average-sized reef in the system consuming three days of a voyage. Each voyage ended when all 10 days had been used and the total number of voyages each year was 25 times the number of available vessels. Again, the 'no crown-of-thorns starfish outbreak' (NCO) option should be regarded as additional to the business-as-usual option.

4.6.4 Rubble stabilisation

Physical disturbances can result in long-lived rubble fields on coral reefs (e.g. Fox and Caldwell 2006). While the formation of coral rubble is a natural part of the dynamics of coral reefs (Hughes 1999), areas of loose rubble are unsuitable for coral recruitment until consolidated. On reefs where the availability of substrate suitable for coral recruitment is limited, interventions that can stabilise rubble may improve the coral resilience of a local, or potentially larger reef network.

We modelled the potential for rubble stabilisation efforts to increase coral condition at both large and fine scale using CoCoNet and ReefMod, respectively. In CoCoNet the formation of coral rubble (as percent cover) was proportional to coral mortality resulting from cyclone and bleaching events. Following disturbances, the cover of loose rubble declined exponentially over five to six years, consistent with observations (Biggs 2013). Each year, varying numbers of coral reefs (20 to 100) were checked in the model for areas of loose rubble and low coral cover (first among highly connected reefs and then randomly). Each year, the stabilisation of up to 1km^2 of loose rubble increased rates of coral recruitment to a maximum of 80 percent of the rate with zero rubble.

In ReefMod, extensive coral mortality following acute disturbances (cyclones, bleaching and crown-of-thorns starfish outbreaks) is transformed into loose coral debris. Coral rubble is generated immediately after cyclones, but only three years after bleaching and crown-of-thorns starfish predation to delay the structural collapse of dead skeletons relative to erosion. Assuming coral recruits do not survive on loose rubble (Fox and Caldwell 2006), the rate of juvenile survival at a given time step is reduced proportionally to the area covered by rubble (see details in Appendix B2).

Loose coral rubble tends to stabilise over time due to natural processes of binding and cementation. We modelled these dynamics using a simple exponential decay function with the assumption that 50 percent of rubble is stabilised over four years which is consistent with empirical observations (Biggs 2013). While rubble stabilisation increases the survival of coral juveniles, this process can be impeded by the addition of new coral fragments following coral mortality events.

Artificial stabilisation of loose rubble on the Reef was modelled by setting rubble cover to 0 percent on reefs targeted for restoration. Simulations (2018–2070) were performed whereby 10 to 20 reefs were restored annually from 2025 onward. The best donor reefs were prioritised for intervention, provided current rubble cover was above five percent in any given year. As for coral deployment, restoration was moved to another reef down the priority list if rubble cover was above this threshold. Restoration effort was estimated every year as the total area of stabilised substratum across the Cairns region.

4.7 Design of intervention modelling to inform benefits streams and cost-benefit analyses

4.7.1 Scenario selection

The outputs of ecological models presented here provided input into economic analyses assessing consequences for benefit streams (T10—Benefit Streams and T9—Cost-Benefit Analysis). For this purpose, we used a systematic construction of scenarios for the model analyses, enabling the role of individual interventions and combined strategies to be explored. We used the subset of interventions that have scope to affect coral condition at large scale, specifically: assisted thermal adaptation of corals, enhanced crown-of-thorns starfish control, and regional solar radiation management. For the completeness of design, we supplemented these interventions with spatial and temporal projections of coral condition under best-practice conventional management, but no RRAP intervention (the counterfactuals), and ran everything under two contrasting climate change scenarios: representative concentration pathways (RCPs) 2.6 and 8.5 adopted by the Intergovernmental Panel on Climate Change (IPCC 2014). Finally, to inform benefits streams and cost-benefit analyses, we also varied the level of effort for each intervention (simulating RRAP resource constraints). The full design is outlined in Table 2.

Table 2: Modelling scenarios used for Reefwide model runs using CoCoNet. CF denotes counterfactual and CBA marks intervention combinations used in the cost-benefit analysis. Low and high levels for 'enhanced corals' represented 10 and 100 million warm-adapted corals outplanted on 100 reefs per year, respectively, and with five-degree heating weeks added thermal tolerance. BAU (business as usual) crown-of-thorns starfish control represented the eight control vessels currently being commissioned on the Reef. Interventions capable of suppressing crown-of-thorns starfish populations to below outbreak density were indicated by 'NCO' (no crown-of-thorns starfish outbreak), also referred to in other RRAP Concept Feasibility Study reports as 'perfect' crown-of-thorns starfish control. Low and high levels of solar radiation management corresponded to 0.3 and 0.7°C cooling during the summer months, lowering cumulative heat stress by ~4 and ~8-degree heating weeks.

ID	Climate (RCP)	Enhanced corals	Crown-of-thorns starfish	Solar radiation management	Comment
1	2.6	Nil	BAU	Nil	CF, CBA
2	2.6	Nil	BAU	Low	
3	2.6	Nil	BAU	High	CBA
4	2.6	Nil	NCO	Nil	
5	2.6	Nil	NCO	Low	
6	2.6	Nil	NCO	High	
7	2.6	Low	BAU	Nil	CBA
8	2.6	Low	BAU	Low	CBA
9	2.6	Low	BAU	High	CBA
10	2.6	Low	NCO	Nil	
11	2.6	Low	NCO	Low	CBA
12	2.6	Low	NCO	High	
13	2.6	High	BAU	Nil	CBA
14	2.6	High	BAU	Low	CBA
15	2.6	High	BAU	High	CBA
16	2.6	High	NCO	Nil	
17	2.6	High	NCO	Low	
18	2.6	High	NCO	High	

19	8.5	Nil	BAU	Nil	CF, CBA
20	8.5	Nil	BAU	Low	
21	8.5	Nil	BAU	High	CBA
22	8.5	Nil	NCO	Nil	
23	8.5	Nil	NCO	Low	
24	8.5	Nil	NCO	High	
25	8.5	Low	BAU	Nil	CBA
26	8.5	Low	BAU	Low	CBA
27	8.5	Low	BAU	High	CBA
28	8.5	Low	NCO	Nil	
29	8.5	Low	NCO	Low	CBA
30	8.5	Low	NCO	High	
31	8.5	High	BAU	Nil	CBA
32	8.5	High	BAU	Low	CBA
33	8.5	High	BAU	High	CBA
34	8.5	High	NCO	Nil	
35	8.5	High	NCO	Low	
36	8.5	High	NCO	High	

4.7.2 Model simulations: Coral dynamics

For CoCoNet, each simulation started in 1951 and ended in 2080, with the first 30 years treated as an equilibration (burn-in) period. Interventions based on conventional management (catchment restoration and enhanced crown-of-thorns starfish control) were deployed from 2021, whereas all new interventions were deployed from 2031. For each intervention strategy (combinations in Table 2), model simulations were repeated 50 times to produce ensembles (Monte Carlo approach). For each run within an ensemble, the initial coral and crown-of-thorns starfish populations were varied by drawing from historical distributions. Environmental forcing was also varied within the prescribed distributions set by the climate scenario (RCP 2.6 or RCP 8.5). This approach provided statistically representative ensembles and allowed us to calculate standard deviations of the mean for individual reefs and to characterise variation among reefs.

Uncertainties arising from environmental forcing (primarily warming and storms) and from ecological processes were propagated through the analyses and captured in simulation ensembles. However, for the purpose of the economic analyses, only the means of ensemble runs (50) for each reef was carried through to the cost-benefit analyses. Therefore, the source of uncertainty reported in economic analyses stems predominantly from among-reef variation.

4.7.3 Model outputs for economic analyses

To inform the estimates of benefit streams, value translations and the cost-benefit analyses, CoCoNet model outputs for the 2096 reefs in the 2001 to 2080 time series were converted to Reef Condition Index (see above). RCI derived from CoCoNet, however, largely represents the state of fast-growing, habitat-forming corals relative to total coral cover because CoCoNet only models two groups and does not explicitly model structural complexity. For economic analyses, RCIs across the Reef domain were partitioned into 157 boxes (each 0.5 degrees latitude by 0.5 degrees longitude, Figure 10). This conversion provided a spatial dataset that enabled consideration of adaptation measures by people and industries dealing with environmental and ecological changes on the Reef under climate change with and without RRAP interventions, including shifts in tourism operations, fishing grounds and consequences for spatial integrity. It also facilitated the calculation of benefit streams within and among regions. Within each geographic box, additional RCI estimates were provided to support economic analyses and the scope for human adaptation. These included RCI weighted by reef size, maximum RCI and numbers of reefs within a box. This, for example, has relevance for the availability of high-RCI reefs above a threshold size (e.g. equivalent to the highly visited Moore Reef in the Cairns region) in an area serviced by tourism and potentially shared by multiple tour operators.

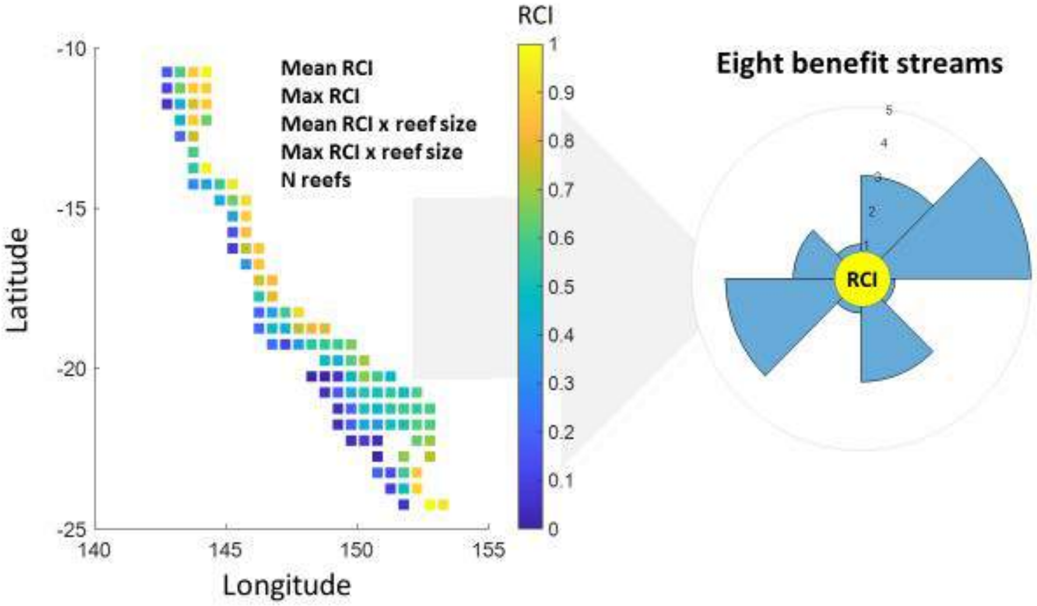


Figure 10: Example output in the spatial Reef grid used for the outputs of Reef Condition Index estimates informing economic analyses.

5. SUMMARY OF FINDINGS

5.1 Counterfactuals for different climate futures

Under assumptions of a low rate of natural adaptation, CoCoNet simulations projected that coral cover in the Reef domain (2096 reefs modelled) would decline under both the Representative Concentration Pathway (RCP) 2.6 and RCP 8.5 (Figure 11A&B). Assuming a higher rate of natural adaptation, however, coral cover may increase under RCP 2.6 around mid-century when global temperatures for this scenario are expected to stabilise (IPCC 2014). Under RCP 8.5, the trajectory of coral cover was projected to be one of precipitous decline throughout the time horizon for both low and high rates of adaptation.

Because the counterfactuals and assumptions around low or high rates of natural adaptation lay the foundation for subsequent analyses of the impact of RRAP interventions for future Reef coral condition, we present the results of two additional sets of analyses: (1) a comparison of coral cover trajectories assuming low and high rates of adaptation for the four Reef sectors, and (2) a comparison of estimated coral cover trajectories by the two ecological models in the Cairns (northern) Reef sector under assumptions of low and high rates of natural adaptation and low and high start states.

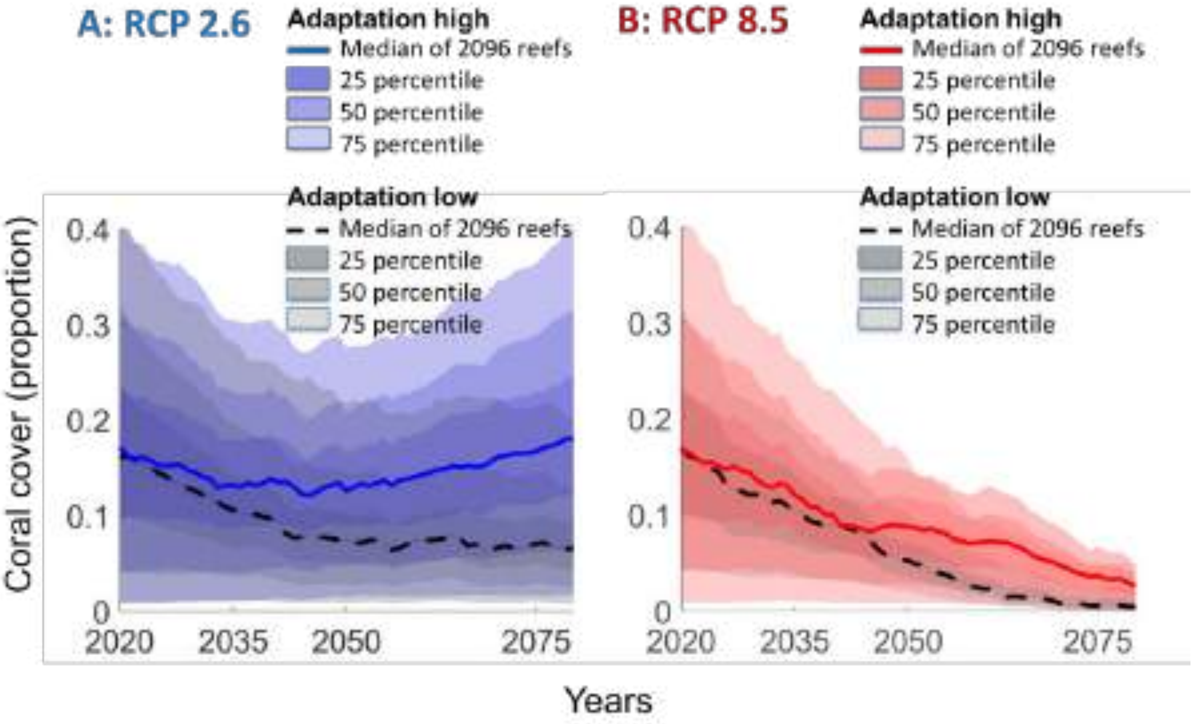


Figure 11: Natural adaptation Reef wide - CoCoNet. Projected trajectories of coral cover on the Great Barrier Reef under moderate (A, RCP 2.6) and severe (B: RCP 8.5) climate change and low (dashed) and high (solid) rates of natural adaptation. Outputs are for CoCoNet for the Reef domain. Data are medians and percentiles for 2096 reefs using the mean of 50 replicate (ensemble) runs for each reef.

Results of the first comparison using CoCoNet indicated marked variation in the importance of rate of natural adaptation between Reef sectors, especially under RCP 2.6. Specifically, in the northern sector (Cairns) the trajectory of coral cover assuming a high capacity for natural adaptation did not diverge significantly from the trajectory assuming low adaptation capacity (Figure 12C). By contrast, the high-adaptation trajectory for southern sector was projected to rise steeply from 15 to 25 percent coral cover during the period 2050 to 2075 under RCP 2.6 (Figure 12G). Further, the projected trajectory for the southern sector, assuming low natural adaptation capacity, declined to lower levels than for the other sectors. Trajectory patterns for the far northern and central sectors under RCP 2.6 were intermediate of those of the northern and southern sectors (Figure 12A-B&E-F).

Under RCP 8.5, the southern sector showed the strongest response to natural adaptation capacity, but only as a temporary reprieve of less than 10 percent coral cover at around 2060 (Figure 12H). One explanation for the stronger response to high adaptation capacity in the South could be that it interacts with the N to S connectivity of warm-adapted genotypes/phenotypes in the northern and far northern sections. In this scenario, high adaptation capacity led to only two to four percent additional coral cover in the other three sectors (Figure 12B, D&F).

In the Cairns region, ReefMod projections for the counterfactuals differed from those produced by CoCoNet (Figure 13). Two key differences were: (1) a high rate of natural adaptation led to a stronger positive response in ReefMod than CoCoNet and (2) CoCoNet showed high rates of recovery from low start state (five percent median cover) with minimal influence from natural adaptation whereas low start in ReefMod led to further decline for both climate scenarios and levels of adaptation (Figure 13G&H).

Importantly, the low start state of five percent median cover is the more relevant current state for the Cairns (northern) sector based on recent reef monitoring observations. However, we analyse the effect of a higher start state to inform decisions around early versus delayed intervention action on reefs with different start states. The efficacy, cost efficiency and ability of one or more interventions to deliver outcomes for Reef values are likely to depend on the system state without intervention (Possingham et al., 2001; Game et al., 2008).

In both models, the low start state of around five percent coral cover in Cairns in 2020 was the result of hindcasting based on the recent (past 10 years) disturbance regime that affected Cairns reefs, including the 2016-17 bleaching events. Without accounting for the 2016-17 bleaching event, the two models have higher start states (~18 percent for CoCoNet and ~ 25 percent for ReefMod).

Importantly, the counterfactual scenarios presented here must not be seen as certain predictions of the future coral cover reef-by-reef. They are tentative projections, under very specific assumptions of coral metapopulation dynamics and forward stress exposure, that provide baseline reef trajectories (i.e. time-series) for assessing the relative efficacy of RRAP interventions. Our focus is on comparing the outcomes of interventions relative to the counterfactuals. Using two models with different formulations, structures and assumptions allows us to consider a wider range of possible scenarios of reef futures. This approach is at the heart of the management strategy evaluation (MSE) or structured decision making in environmental management and conservation.

Note: In our analyses using CoCoNet in the remainder of this report, we assumed low capacity for natural adaptation. Our rationale is partly that high rates of adaptation as modelled by CoCoNet simulations are untested. Assuming high rates of adaptation, in combination with ocean acidification being excluded from analyses (see above), may lead to unrealistically optimistic projections of coral condition for the counterfactual under climate change.

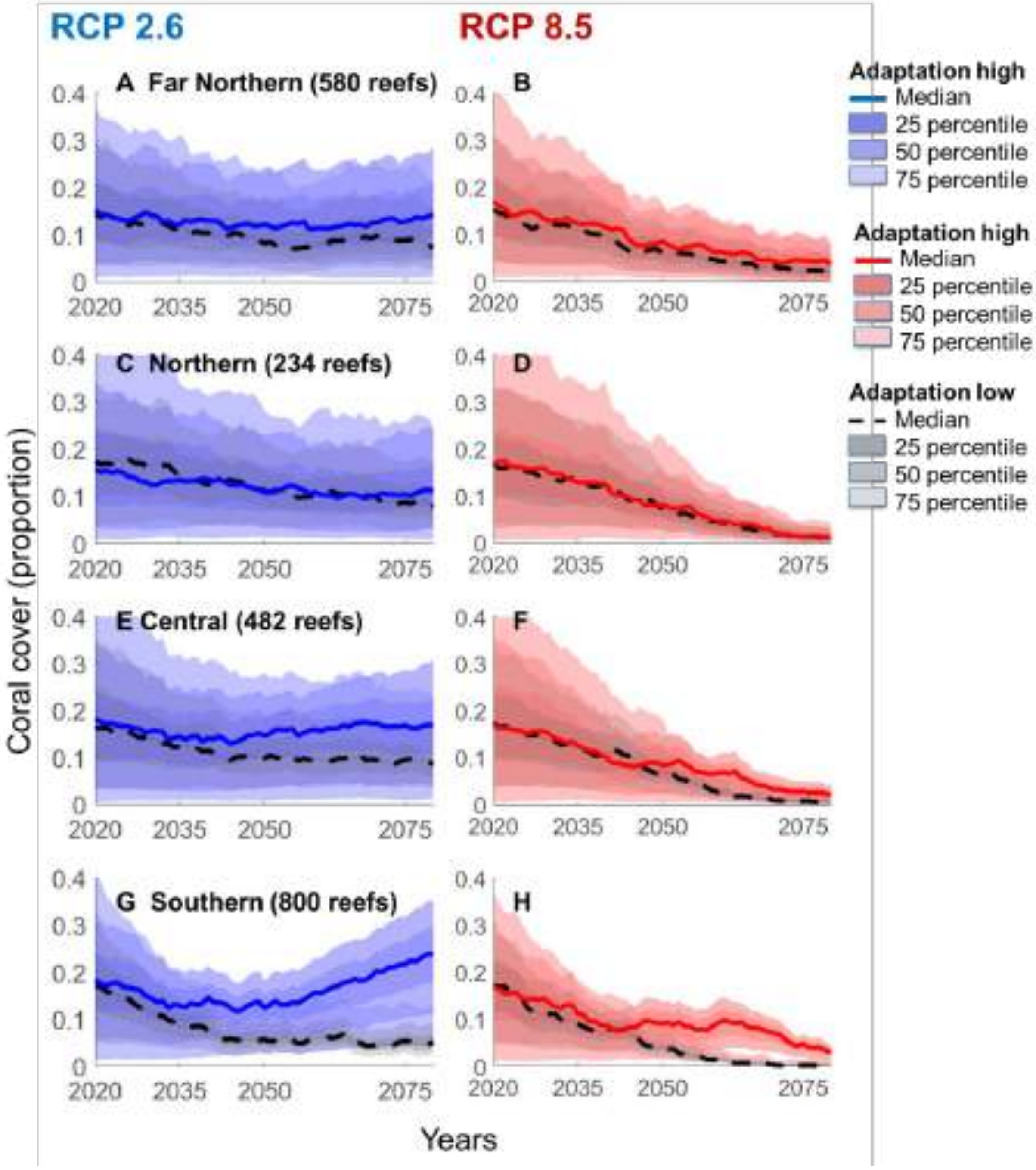


Figure 12: Reef counterfactuals by Great Barrier Reef sector: estimated trajectories of coral cover by CoCoNet for the four Reef sectors under assumption of high and low rates of adaptation and under moderate (RCP 2.6) and severe (RCP 8.5) climate change. Data are medians and percentiles as indicated in the legend. Mean coral cover per reef was estimated by 50 replicate (ensemble) runs.

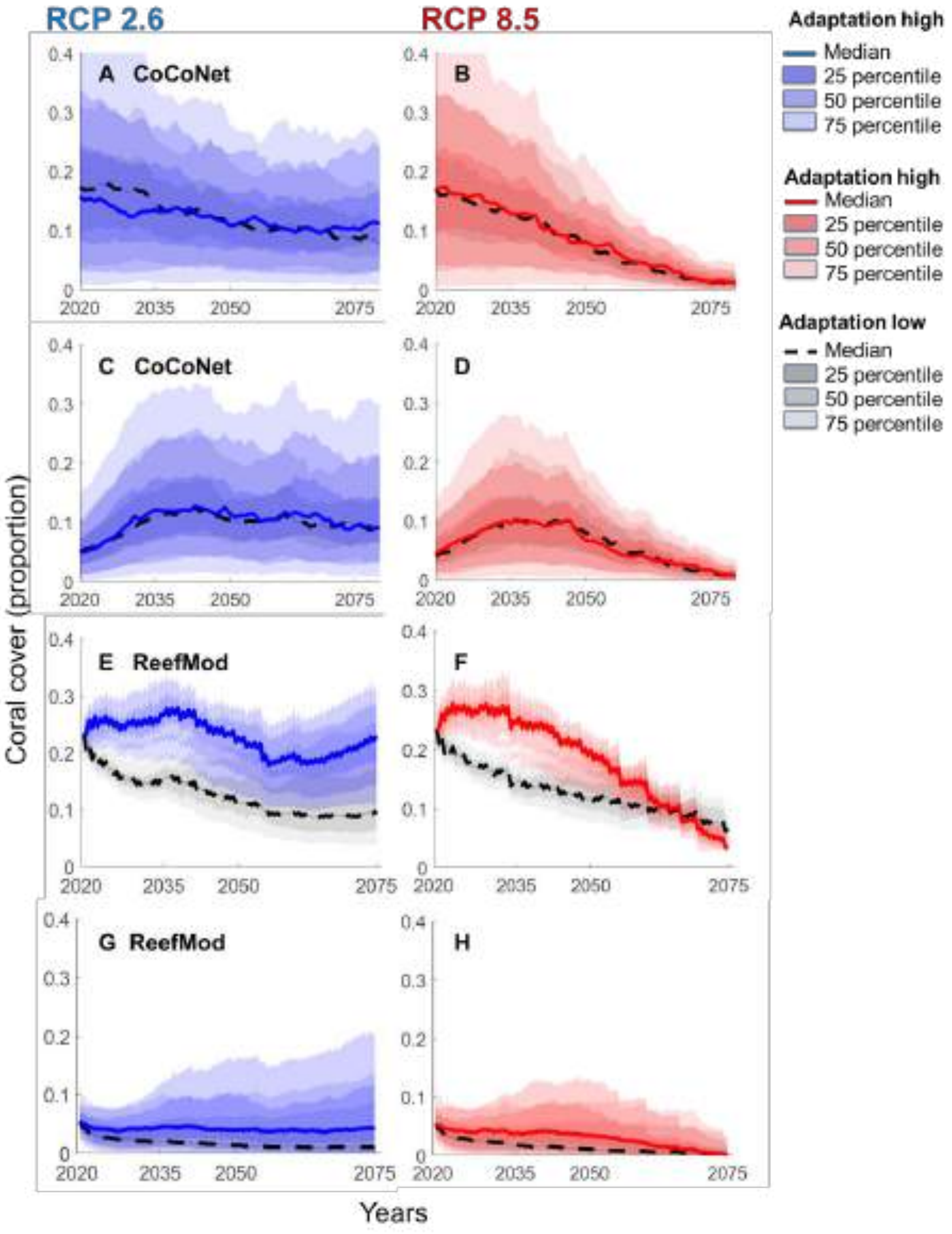


Figure 13: Adaptation model comparisons for counterfactuals in the northern (Cairns) sector under assumptions of low and high capacity for natural adaptation (legend), contrasting climate change scenarios (columns) and high versus low start states (rows). Specifically, CoCoNet was forced to five percent average coral cover in 2017 as predicted (hindcast) by ReefMod and vice versa. Data are medians and quartiles for 234 (A-D, CoCoNet) and 156 (E-H, ReefMod) reefs established by 50 (CoCoNet) or 40 (ReefMod) ensemble runs. The sawtooth pattern for ReefMod results is driven by seasonal (six-monthly) variation.

5.2 Rubble stabilisation

5.2.1 CoCoNet

To analyse effects of rubble stabilisation using CoCoNet, we estimated absolute rather than proportional coral cover because absolute cover better reflects the intervention of making more habitat available for coral colonisation. Absolute coral cover was estimated coarsely by assuming that shallow coral real estate (hard reef substrate in less than 10m depth) accounts for approximately 10 percent of total reef area.

Results of simulated rubble stabilisation in CoCoNet for 20 and 100 reefs distributed along the Reef showed inconclusive effects for both RCP 2.6 and RCP 8.5 (Figure 14). Specifically, the annual stabilisation of 1km^2 rubble did not cause a net shift of reefs into higher categories of absolute coral cover. Conversely, there was a tendency for the opposite trend under RCP 8.5. A possible driver of this discrepancy is the variation between counterfactual and intervention ensembles.

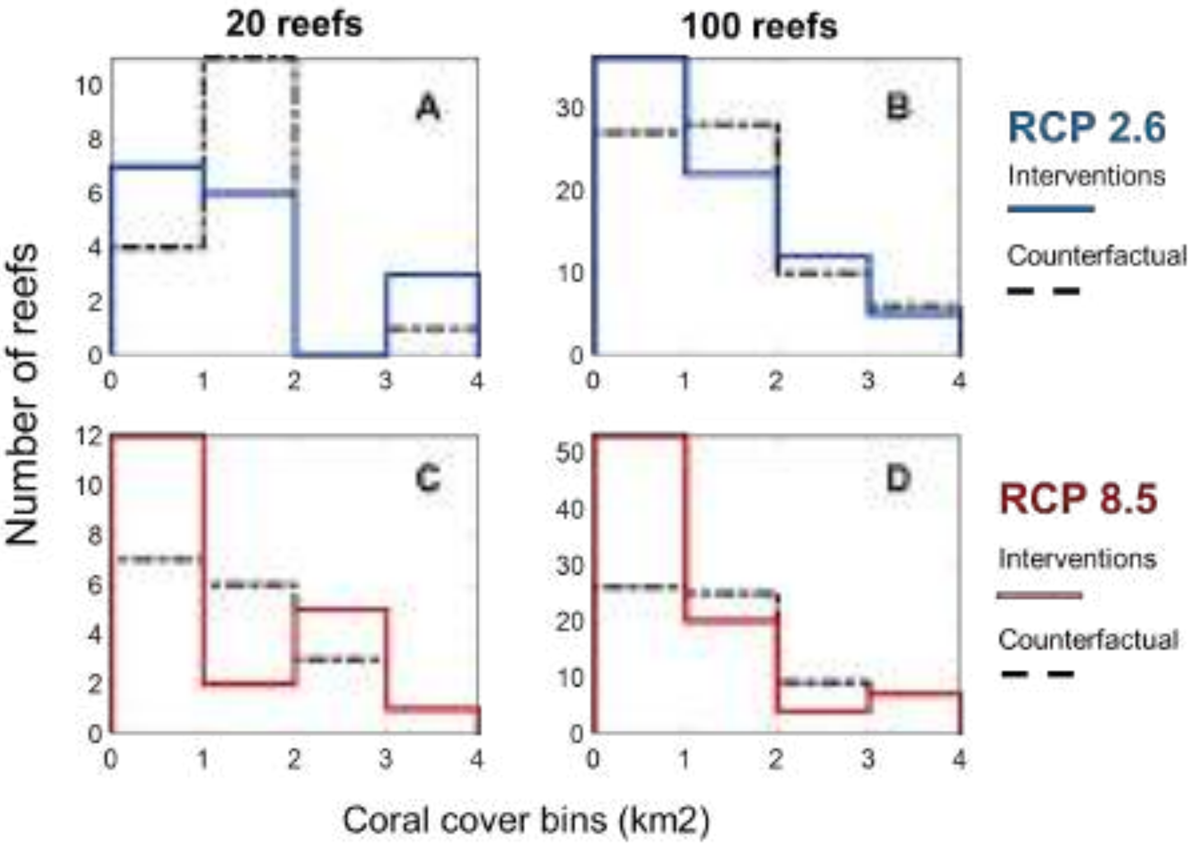


Figure 14: Rubble stabilisation – CoCoNet results. Panels show distributions of reefs with varying absolute coral cover (percent cover multiplied by area of coral habitat). Note different scales on y-axes.

5.2.2 ReefMod

Under RCP 2.6, and assuming low adaptation potential, ReefMod results showed that rubble stabilisation had no detectable effect on the regional coral cover (Figure 15A). Being generated from coral loss after disturbance, rubble cover remained low within the Cairns sector (max. ~10 percent) due to low coral cover (max. ~10 percent) maintained on all reefs over the course of simulations. Hence, the stabilisation of small rubble beds (i.e. five to 10 percent rubble cover) had limited impact on the survival of juvenile corals, a condition close to optimum. Once a reef is restored and rubble cover set to 0 percent, it takes a long time before rubble exceeds five percent again because physical disturbances can only generate limited amounts of rubble at a time, and most of it is rapidly stabilised by natural processes of consolidation. As a result, reefs selected for intervention largely extended beyond the priority list of well-connected reefs, with many substitute reefs visited multiple times.

Conversely, rubble stabilisation had higher efficacy under RCP 2.6 and assuming high adaptation potential (Figure 15C). This was because corals achieve greater cover and so produce more loose rubble following disturbances. This slight increase in the production of rubble (maximum covers around ~15 percent) was enough to affect coral demographics negatively which could be mitigated by rubble stabilisation. While this highlights that loose rubble has a greater impact where corals are abundant, it merely reveals the magnitude of the negative feedback that impedes coral recovery. One important implication is that healthy reefs today are likely to benefit the most from rubble stabilisation post-disturbance. It is certainly more cost-efficient to focus intervention on reefs where rubble is abundant rather than dispersing the restoration effort. Moreover, it can be anticipated that much greater regional benefits might be achieved with a strategy that optimises the sequence by which reefs are selected for rubble stabilisation. In particular, the threshold value of rubble cover used to trigger intervention is likely to have a disproportionate effect on the benefits measured at the scale of the region. Importantly, the impacts of rubble stabilisation can be overlooked in cost-benefit analyses based on pessimistic reef state projections, i.e. the ‘rubble problem’ is contingent on the amount of corals available (the source of rubble) prior to disturbance.

Under RCP 8.5, rubble stabilisation had no discernible effect on coral cover under any assumption of adaptation and deployment strategy (Figure 15B and D). Similar to the RCP 2.6 scenario of low adaptation potential, reefs in the Cairns sector maintained such low levels of coral cover that disturbances did not create enough rubble to affect juvenile coral survival.

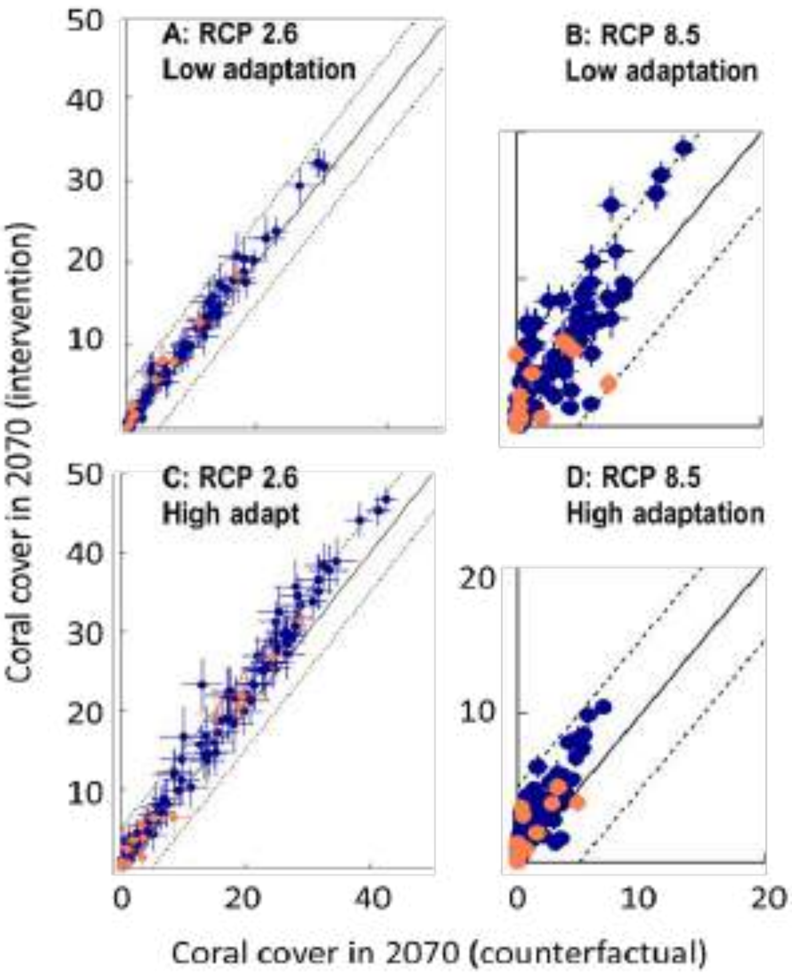


Figure 15: ReefMod: simulated impact of rubble stabilisation for 20 reefs in the Cairns sector under projections of (A&C) moderate and (B&D) unmitigated climate change and low (A&B) and high (C&D) rates of adaptation. The graph shows distributions of coral cover (relative) on all 156 coral reefs in the sector with (y-axis) and without rubble stabilisation implemented (counterfactual, x-axis). Orange markers indicate priority reefs targeted for rubble stabilisation based on their connectivity in the reef network. 'Stabilisation effort' here refers to the effort of the intervention to stabilise loose rubble measured as total area stabilised in a given year. Error bars indicate SD of reef coral cover over 40 replicate runs. The continuous line represents equality between the counterfactual and intervention projections, so that a reef standing on this line is projected to exhibit the same coral cover under both scenarios. Reefs positioned above this line tend to perform 'better' under intervention as their projected coral cover is greater than the counterfactual projection. Dotted lines indicate a difference of ± five percent coral cover relative to help visualising the ecological significance of intervention benefits.

5.3 Effects of major interventions – temporal patterns

In the following we present the results of simulations examining the efficacy of the larger-scale interventions, specifically the outplanting of corals with enhanced thermal tolerance (enhanced corals, EnC), regional solar radiation management (SRM) and additional crown-of-thorns starfish control leading to full suppression of outbreaks (no CoTS outbreaks, NCO). We examined these using different approaches. Enhanced corals were included here instead of rubble stabilisation because the injection of genotypes with increased thermal tolerance is likely to provide more direct flow-on effects to the larger reef network through connectivity.

First, we analysed the efficacy of individual interventions and their combinations relative to counterfactuals (one for each climate change scenario) as time series for all reefs. This was to provide initial insight into the potential scale of ecological benefits emerging from different intervention strategies. Second, we examine how impacts are predicted to play out spatially – for each of the four management areas. Finally, we examine how interventions might shift the distributions of coral conditions over different time horizons. For clarity, we limit the presentation of results to no (i.e. turned off) versus high levels for individual interventions and their combinations. This allows for a bounded approach to considering the benefits of the interventions – if little effect can be seen when contrasting these ‘strong’ alternatives (none vs high) then it is relatively safe to assume that a low setting would show marked benefits. This reduces the need to explicitly consider a broad range of alternative settings to cover many different levels of effect that may result due to various limiting factors.

Projections of coral cover for all modelled Reef reefs using CoCoNet showed an only marginal impact of outplanting warm-adapted coral juveniles as a single intervention for both RCP 2.6 (Figure 16A-G) and RCP 8.5 (Figure 16H-N). Note that results in both sets of panels are for high start states and high levels of interventions in Table 2, i.e. in this case 100 million corals outplanted per year. While the median of this intervention is indistinguishable from the counterfactual over time, the 75 percentile of the intervention extends above the 75 percentile of the counterfactual after around year 2050. This means the coral cover of some reefs benefit from the enrichment of hardier corals. We analyse this in more detail below.

Cooling and shading (assuming high-efficacy, Table 2) as a single intervention produced a strong and sustained response for RCP 2.6 (Figure 16B) and a strong and tapering response for RCP 8.5 (Figure 16I). Specifically, high-efficacy solar radiation management by itself showed scope to double coral cover relative to the counterfactual for RCP 2.6, and elevate coral cover by 7-10 percent (in absolute terms) relative to the counterfactual under RCP 8.5.

Suppressing crown-of-thorns starfish to the extent that there is outbreak prevention (as a single intervention, NCO) also interacted with climate change. Specifically, under RCP 2.6, the benefit for coral cover from perfect crown-of-thorns starfish control was predicted to grow over time (Figure 16C). Conversely, the benefit of controlling crown-of-thorns starfish perfectly under RCP 8.5 is likely to be marginal (Figure 16J), as crown-of-thorns starfish population outbreaks may be limited by the overall decline in their prey (coral). Similar to enhanced corals, however, the 75 percentile of NCO under RCP 8.5 extends above that of the counterfactual from 2050 and onwards, indicating that some reefs benefit from NCO as a single intervention (Figure 16J).

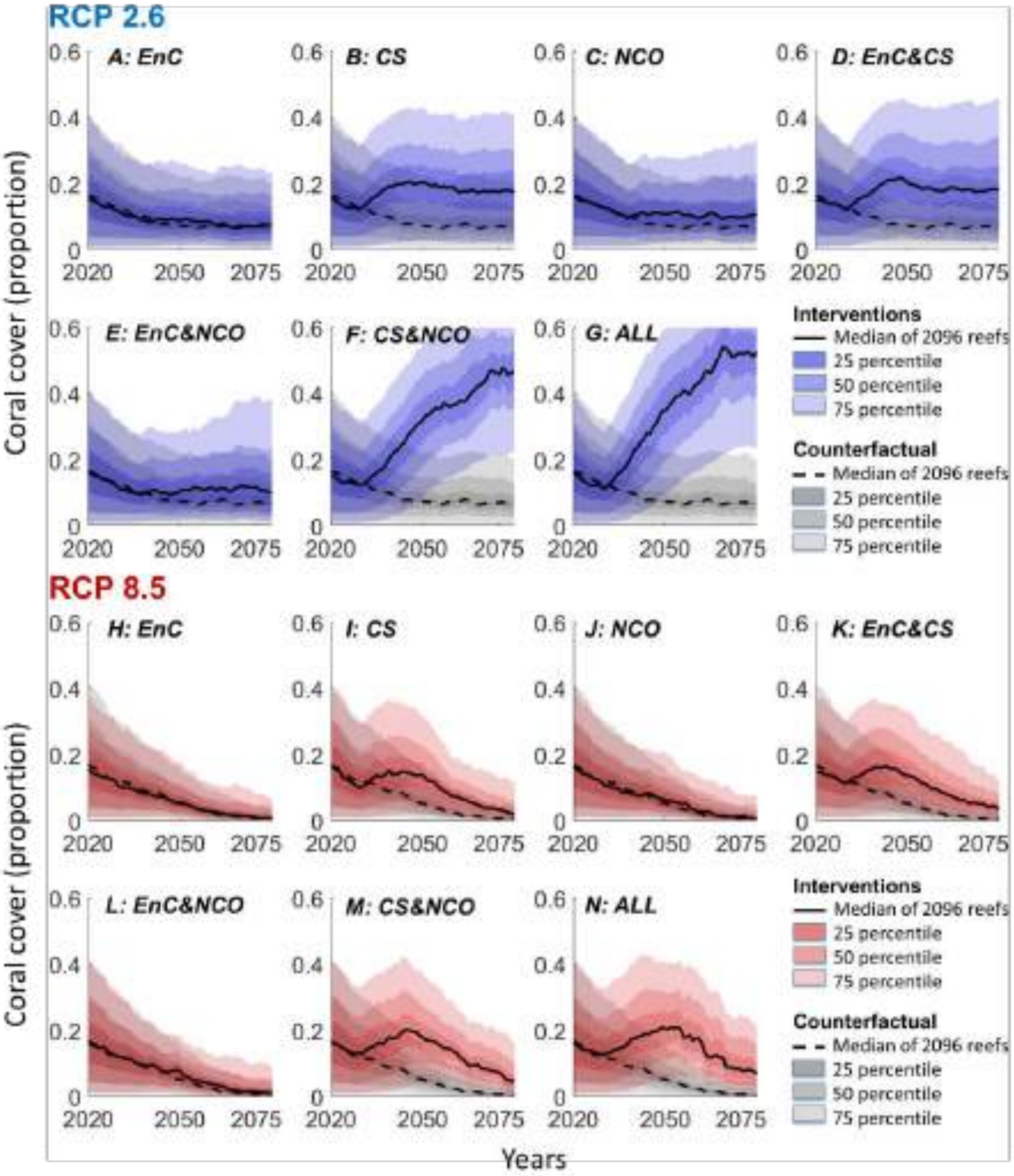


Figure 16: Projections of coral cover for interventions (solid line, blue envelopes) and the counterfactual (dashed line, grey envelopes) under RCP 2.6 based on CoCoNet simulations. EnC: enhanced corals; CS: cooling and shading; NCO: no crown-of-thorns starfish outbreaks. Data are medians and quartiles for 2096 reefs with 50 ensemble runs to establish the mean coral cover for individual reefs in a given year. Interventions begin in year 2031.

A question emerging from the comparison of the impacts of individual interventions is whether these interventions synergise (interact positively) when deployed in combination as strategies. If so, then this will have implications for the efficacy and cost-efficiency of strategy designs in the RRAP R&D Program. We show this informally by comparing the results of individual interventions added with the results of all interventions deployed in combination. We illustrate this here simply by comparing the sum of differences between interventions and counterfactual in Figure 16A-C versus Figure 16G for RCP 2.6 and Figure 16H-J versus Figure 16N for RCP 8.5. We note that a more formal analysis for estimating synergies is given in Bozec and Mumby (2014).

Results suggest two points. First, the combination of cooling and shading (CS) and suppression of crown-of-thorns starfish (NCO) appear to synergise for both RCPs. Second, combinations of enhanced corals with solar radiation management (EnC+CS), and enhanced corals with no crown-of-thorns starfish outbreaks (EnC+NCO), do not perform better (potentially worse under RCP 2.6) than the sum of individual interventions (Figure 17). Consequently, the potential synergy of all three interventions (right-most bar in Figure 17) is likely driven by the solar radiation management-NCO interaction, or by inclusion of enhanced corals in a 3-way interaction (see below).

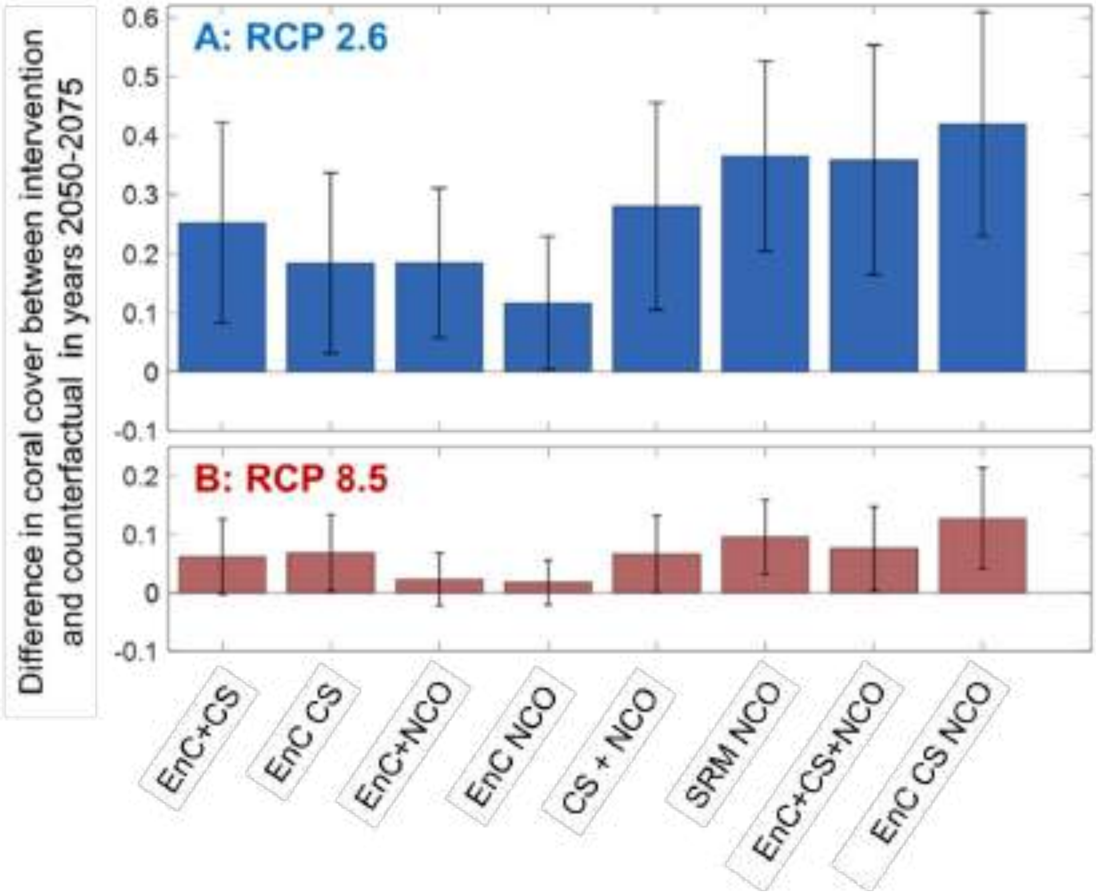


Figure 17: Interactions between interventions in years 2050-2075 for (A) RCP 2.6 and (B) RCP 8.5 for all Reef reefs (CoCoNet simulations). The + sign indicates that the results of single interventions were added (to allow for assessment of whether combined interventions had better than additive outcomes. For example, HC+CS is the additive outcome of the individual actions of HC and the CS, whereas HCCS is the result of running both intervention strategies in combination. Data are means and SD of 2096 reefs.

5.3.1 Impacts of interventions within time-periods

The large variation among reefs within counterfactuals and intervention strategies raises the question: (1) how do interventions shift the distribution of coral covers among reefs? While the trend in coral cover over time is informative in terms of assessing whether RRAP can stem coral decline at the Reef scale, it does not give insight into the extent to which coral cover can be sustained or improved on subsets of reefs. The latter is likely to be an important secondary objective where large-scale trends cannot be counteracted, but where the allocation of restoration and adaptation efforts to local small-scale interventions can sustain clusters of reefs that provide valuable ecosystem services.

We examine this question by comparing the distributions of reef conditions between counterfactuals and interventions in the time window between years 2051 and 2060. In other words, we take a 10-year time slice of coral covers for the seven intervention strategies in Figure 16. We use the mean coral cover for each reef within this window to represent a decade rather than an individual year.

Further, we compare two analyses: one based on the areal proportion of coral cover for a given reef, and one based on absolute coral cover per reef. Proportional live coral cover relative to available coral habitat is the predominant metric used in surveys including in all analyses above. Absolute coral cover per reef, however, may be more informative for reef restoration and adaptation programs where intervention efforts and resourcing as well as benefits from ecosystem services scale more with absolute rather than with relative coral cover.

Results of these analyses using proportional coral cover show that all interventions shift reefs into higher categories of cover (Figure 18). Again, the pattern is driven mostly by solar radiation management in both climate scenarios. Specifically, in intervention combinations involving solar radiation management, a large number of reefs that in 2051-2060 had lower than 20 percent coral cover in the counterfactual, moved to higher categories of relative coral cover under RCP 2.6 (Figure 18 D&F). The pattern was similar under RCP 8.5, expect that a large shift occurred on reefs that had less than 10 percent coral cover in the counterfactual (Figure 18K&M). The total number of reefs that shifted to higher categories of relative coral covers in interventions involving solar radiation management ranged from 734 to 1247 (more than half the modelled reefs) under RCP 2.6 and 699 to 1172 under RCP 8.5 (Table 3A).

Interestingly, while enhanced corals (HC) as a single intervention was projected to shift between 68 (RCP 8.5) and 183 (RCP 2.6) reefs to higher categories of relative coral cover (Table 3A), it did not add efficacy when combined with perfect crown-of-thorns starfish control. In other words, simulated efforts to stop crown-of-thorns starfish outbreaks (NCO) were not helped by including enhanced corals in a combined intervention (EnCNCO). Conversely, combining solar radiation management with no crown-of-thorns starfish outbreaks NCO improved the relative coral cover on more reefs than for the sum of individual interventions (Table 3). Adding enhanced corals to the CSNCO combination (EnCCSNCO) led to fewer reef shifting to higher coral cover under RCP 2.6 and more reefs under RCP 8.5.

Finally, analyses of shifts in the distribution of reefs as a function of absolute coral cover (as km^2 live coral) suggested that the reefs that shifted to higher categories of absolute coral cover were mainly reefs with coral habitat areas larger than 0.5 km^2 (Figure 19). Significant shifts of smaller reefs of the intervention combinations involving solar radiation management are partly obscured by the log scale of Figure 19. Note, for clarity we here limit analyses to the majority of reefs in the size range of 0 to 4 km^2 (of coral habitat area only).

Two key findings emerged from the analysis of distributions of absolute coral cover. Firstly, the CSNCO combination shifted five-fold more reefs into higher categories of absolute coral cover than other combinations (HCCS, HCNCO; Table 3B). Secondly, the addition of enhanced corals to the CSNCO combination (HCCSNCO) led to 53 more reefs (265 -212) improving absolute coral cover under RCP 2.6, and a near–doubling of the number of reefs (85 to 142) that shifted to higher absolute coral cover under RCP 8.5. The latter suggests that intervention efficacy as measured by absolute improvements in coral cover may depend on multiple interventions cooperating.

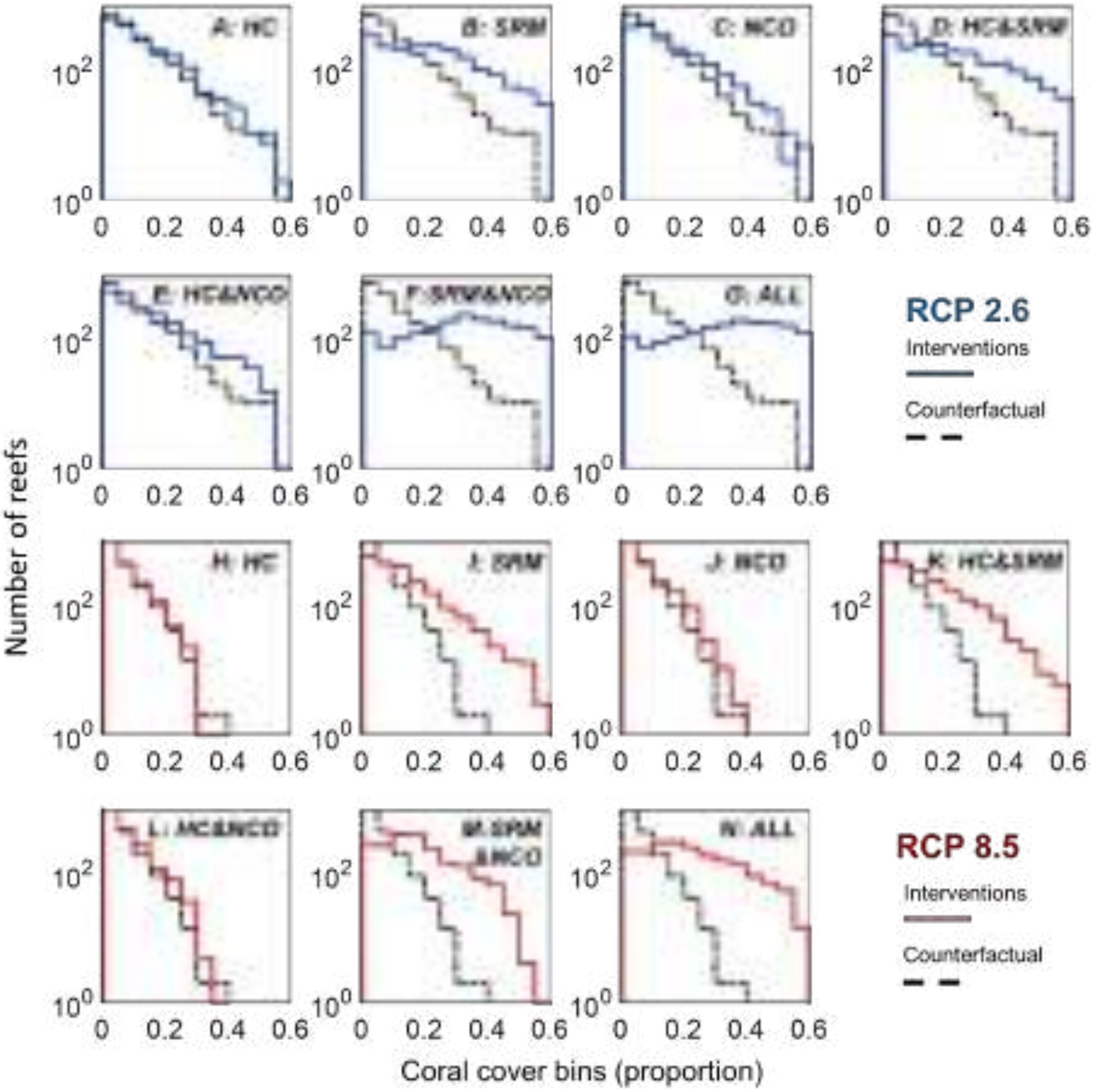


Figure 18: Distributions of coral reefs (N = 2096) as a function of relative coral cover in years 2051-2060 under RCP 2.6 (blue) and RCP 8.5. Interventions and counterfactuals are similar to those in Figure 16.

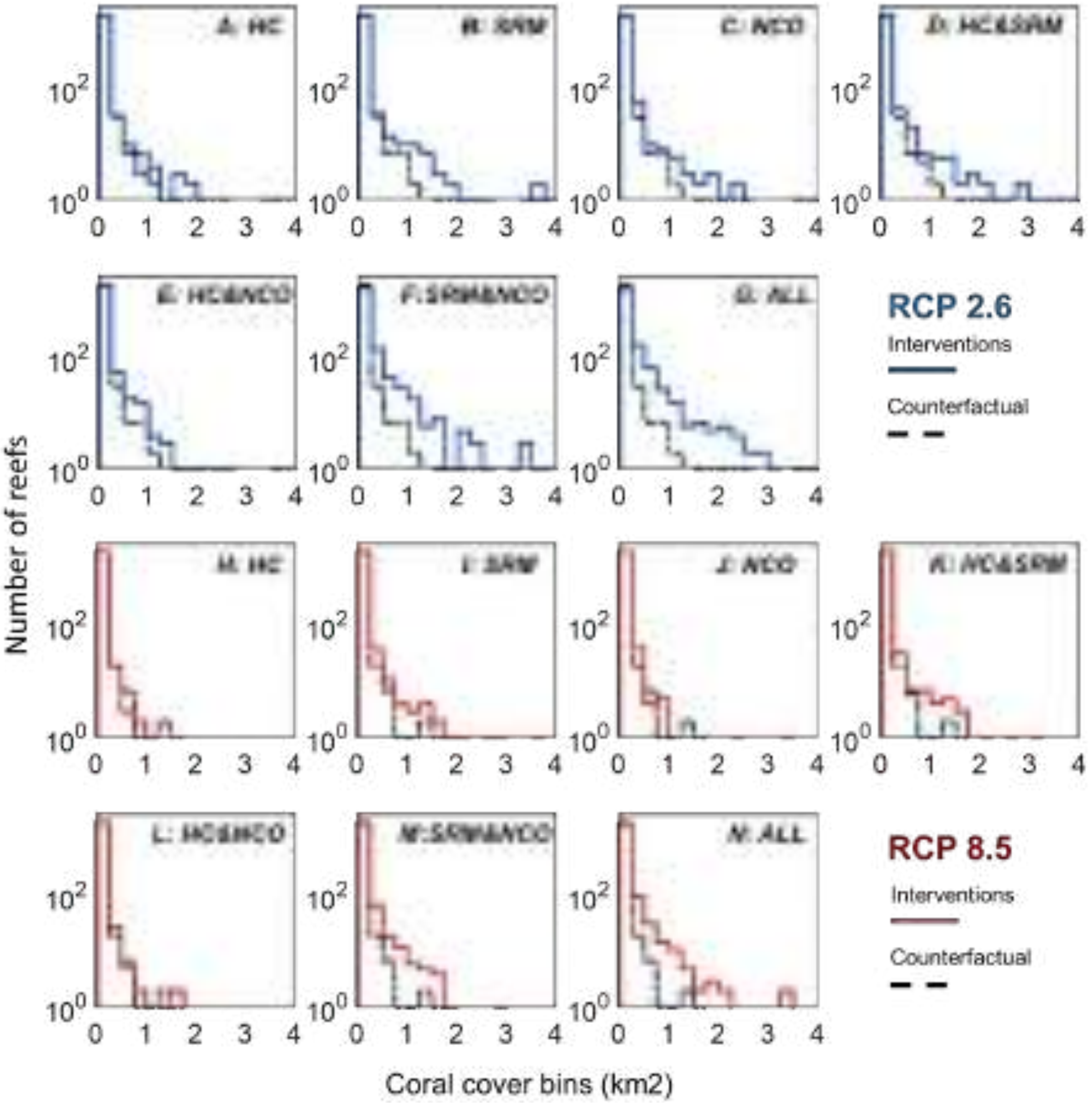


Figure 19: Distributions of coral reefs (N = 2096) as a function of absolute coral cover in years 2051-2060 under RCP 2.6 (blue) and RCP 8.5. Interventions and counterfactuals are similar to those in Figure 18.

Table 3: Total number of reefs that move to higher categories of coral cover in Figure 18 and Figure 19. EnC: enhanced corals; CS: cooling and shading; NCO: no crown-of-thorns starfish outbreaks.

		Interventions						
Cover	**Scenario**	EnC	CS	NCO	EnC CS	EnC NCO	CS NCO	EnC CS NCO
A: Relative (prop)	**RCP 2.6**	183	734	348	726	359	1247	1152
	RCP 8.5	68	699	231	791	231	1172	1296
B: Absolute (km2)	**RCP 2.6**	12	34	42	45	52	212	265
	RCP 8.5	7	36	26	30	11	85	142

5.4 Effects of interventions – spatial patterns

The large variation around the estimates of coral cover in temporal projections (Figure 16) are partly attributed to spatial variation in the responses of reefs within regions. In turn, this variation is the result of spatial and temporal changes in connectivity patterns on the Reef driven by meteorological and oceanic forcing and by the stochasticity of cyclones, thermal anomalies, crown-of-thorns starfish outbreaks, and by water quality.

In this section we illustrate the temporal as well as spatial behaviour of an example intervention strategy. We show these patterns for each of the four management areas separately to enable exploration of intra and inter-regional behaviours. Further, we show results as the difference in coral cover between intervention and counterfactual (ΔCover), in other words the difference between solid and dashed lines in Figure 16. We focus on the enhanced coral/solar radiation management/no crown-of-thorns starfish outbreaks combination under RCP 8.5 an example as it illustrates the temporal complexity that can be expected under severe climate change.

To inform discussions around how ecological returns on efforts are distributed spatially in absolute terms (i.e. as absolute gain in coral cover), we show spatial and temporal results as differences in relative coral cover multiplied by the size of the coral habitat area on each reef. This conversion has implications for analyses of the extent to which RRAP might impact on the quality and quantity of the coral reef real estate in a reef cluster, within a region, or Reefwide. These considerations of how absolute gain in coral cover are affected have implications for intervention costs, as well as the associated ecosystem services and benefit streams that are functions of both reef size and quality. Spatial patterns of ΔCover were calculated as the ensemble mean for the full intervention combination minus the ensemble mean for the counterfactual.

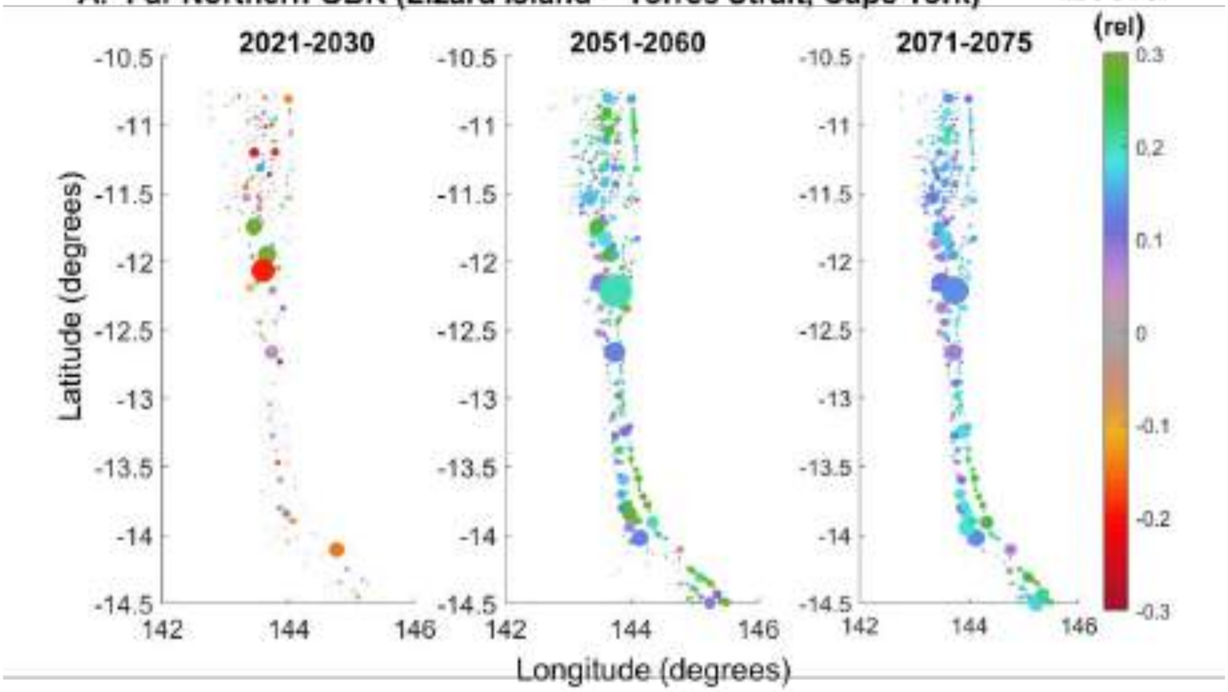
Results showed that differences in coral cover between intervention and counterfactual are projected to vary markedly within and between sections in year 2020 (Figure 20). Note that bubble sizes in Figure 20 represent changes in absolute coral cover between intervention and counterfactual, whereas colours indicate change in relative coral cover including direction of change. The distributions in the leftmost panels in Figure 20 show variation attributable to CoCoNet ensemble runs only as simulation of interventions occurring after 2020. This source of variation was most prominent for the far northern and the central sections (Figure 20 A and C).

Two key findings were: (1) absolute changes in coral cover (bubble sizes) tend to decline from north to south in 2051-60 and 2071-75, and (2) among-reef variation declined over time. One exception were reefs in the Capricorn Bunker Group (far southern Reef), were absolute and relative coral cover were maximised in 2051-60, but with some sustained cover in 2071-75 (Figure 20D).

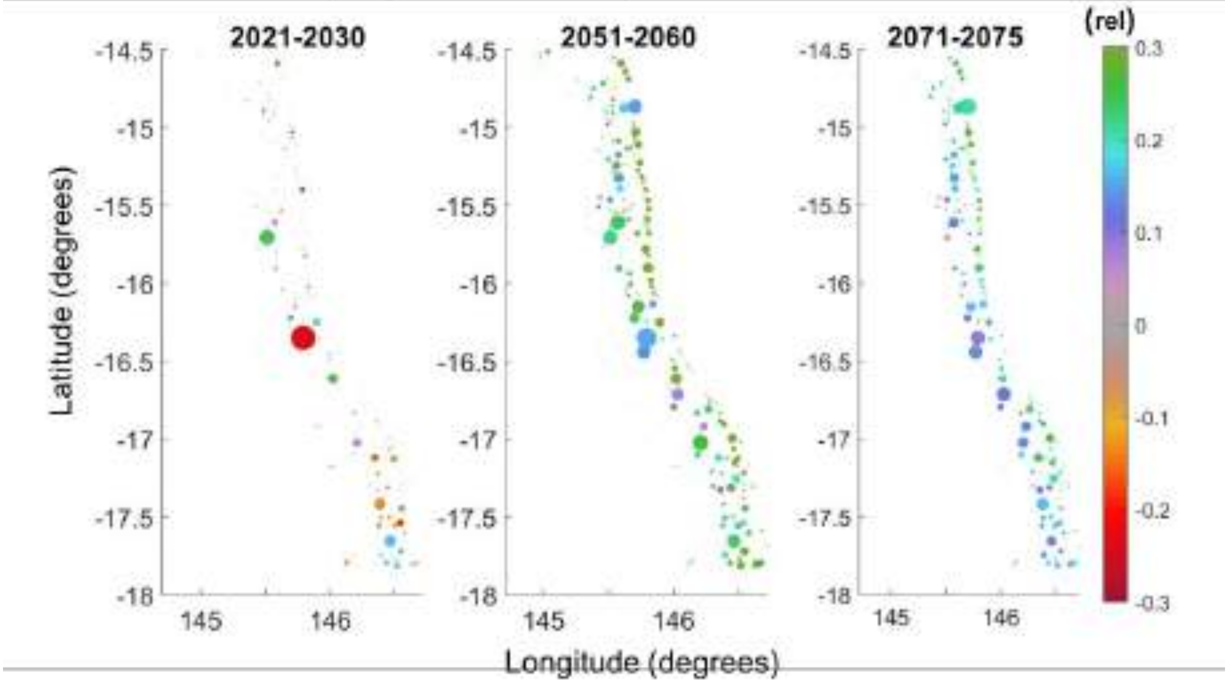
The greater positive difference in relative coral cover between counterfactual and intervention in the Far North is consistent with results in (Figure 16), but it is surprising that absolute gains in coral cover by intervention are nearly sustained out to 2075. In contrast, absolute differences in coral cover between intervention and counterfactual in the Swains (NE part of the southern Reef, Figure 20D) are small compared to the other sectors.

The decline in variation over time is consistent with the pattern in Figure 16. We propose that this decline in spatial variation over time could be driven by at least three processes. Firstly, system-wide decline in coral cover caused by severe climate change (RCP 8.5) is likely to suppress variation in coral condition among reefs. Secondly, intervention effects and climate forcing gradually exceed random variations over time. Finally, by targeting source populations in the simulations of the outplanted corals with enhanced thermal tolerance, concomitant with the targeting of source reefs for crown-of-thorns starfish control (Hock et al. 2016, 2017), interventions drive the enhanced dispersal of corals, and suppressed dispersal of crown-of-thorns starfish, to reefs downstream in the network.

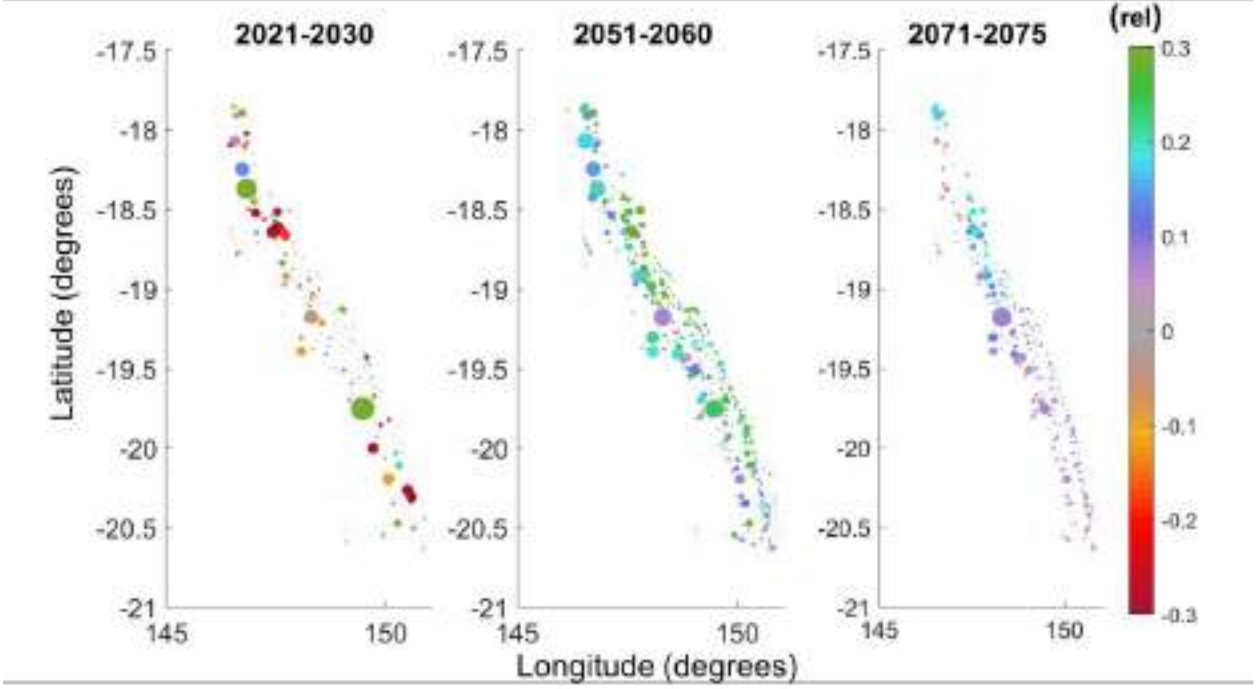
A. Far Northern GBR (Lizard Island – Torres Strait, Cape York)



B. Northern GBR (Tully – Lizard Island)



C. Central GBR (Mackay – Tully)



D. Southern GBR (Bundaberg – Mackay)

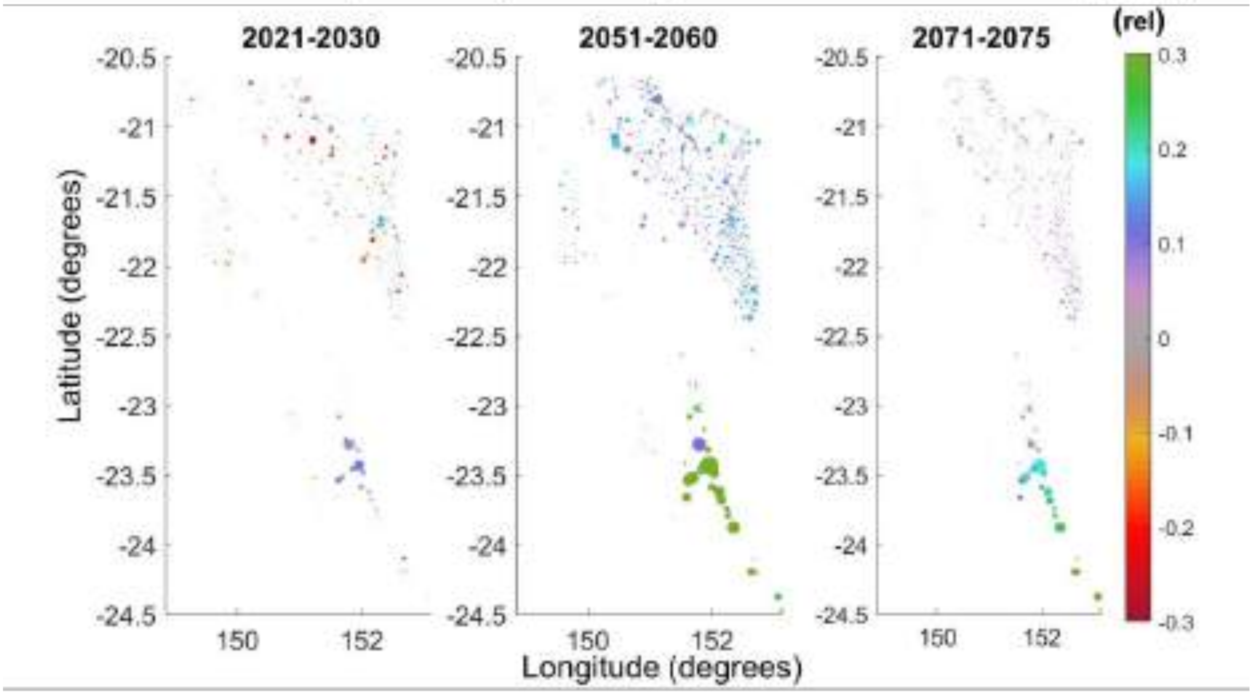


Figure 20: Projected spatial and temporal differences in absolute (bubble sizes) and relative (colour scale) coral cover between intervention and counterfactual of enhanced corals, solar radiation management and full suppression of crown-of-thorns starfish outbreaks under RCP 8.5, across four Reef regions (A-D). Negative differences in year 2020 are due to variation between ensemble means for interventions and counterfactuals for CoCoNet. Note that bubble sizes are not to scale. Interventions begin in year 2031.

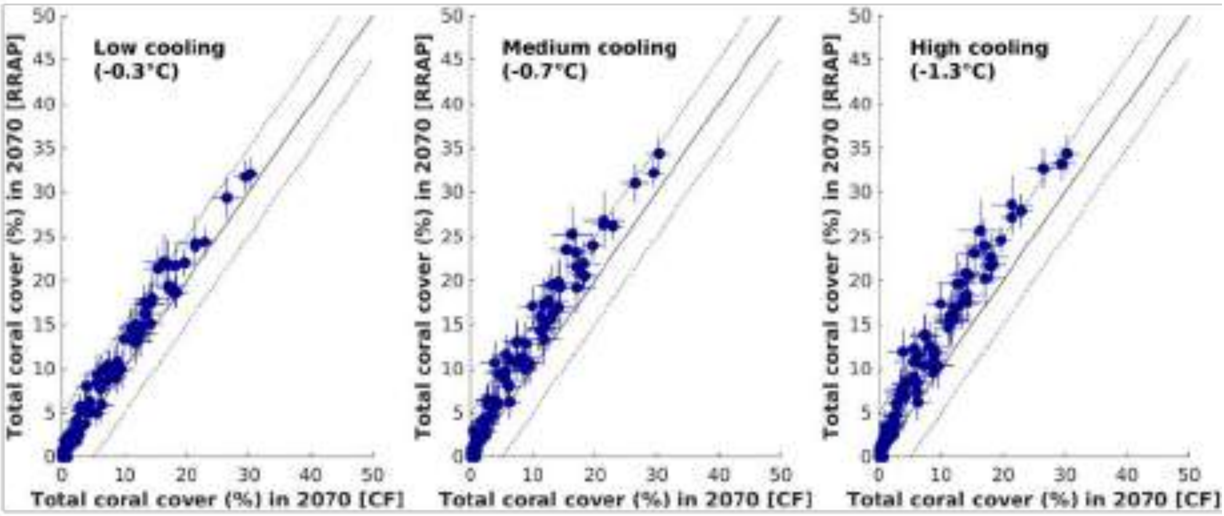
5.5 Regional/local-scale response

5.5.1 Regional cooling and shading

Results above for CoCoNet show that cooling and shading is the single intervention that is likely to produce the strongest coral response. To test for consistency in results across models we here also present results of model simulations with regional cooling and shading using ReefMod. These analyses were run with similar assumptions as for CoCoNet, regarding the deployment of solar radiation management (year 2031 onwards, applied for 12 consecutive weeks during the warmest summer months), but explored for an extended range of solar radiation management efficacies: 0.3, 0.7 and 1.3°C cooling of Reef surface waters in the Cairns region. These correspond to the lowering of cumulative heat stress during the summer bleaching season by 3.6, 8.4 and 15.6 degree heating weeks, respectively, relative to the genetically-determined optimum temperature of each coral. It is important to note that the uppermost solar radiation management scenario employed is likely to be extreme (see **T14—Environmental Modelling of Large-scale Solar Radiation Management**). It is equivalent to reducing the incoming shortwave solar radiation by an average of around 57 Wm^{-2} (17 percent) over the entire Reef for the three-month summer period.

Results of ReefMod simulations were consistent with those of CoCoNet for the intermediate level (0.7 °C or 8.4 degree heating weeks): solar radiation management led to a largely consistent increase in coral cover relative to the counterfactual for both RCP 2.6 and 8.5 (Figure 21). Interestingly, even the lowest efficacy level of 0.3°C cooling led to a near-consistent benefits in terms of increased coral condition under both climate scenarios. This level of cooling is potentially achievable as it is equivalent of five Wm-2 (~1.5 percent) of incoming solar radiation across the Reef during summer (**T14—Environmental Modelling of Large-scale Solar Radiation Management**). Results shown here are for low rates of adaptation to match the level used consistently for CoCoNet.

A: RCP 2.6 – low rate of adaptation



B: RCP 8.5 – low rate of adaptation

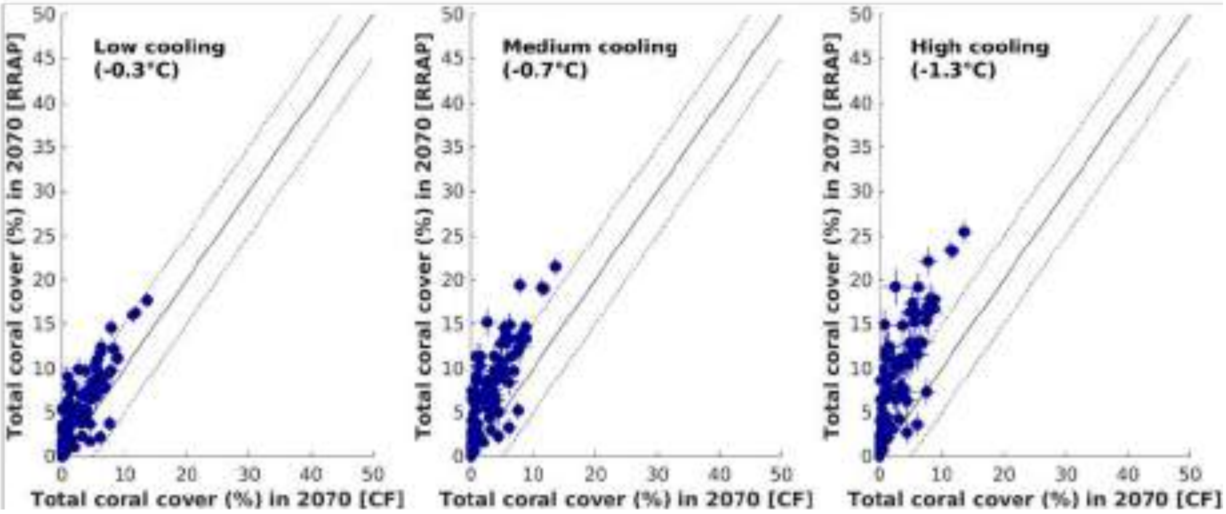


Figure 21: Long-term shifts in coral condition (coral cover) between the counterfactual (x-axis) and under three levels of solar radiation management (y-axis) under Representative Concentration Pathway (RCP) 2.6 (A) and RCP 8.5 (B) based on ReefMod simulations. Results are produced by ReefMod for the Cairns section of the Reef. Vertical and horizontal error bars are standard deviations of the mean for individual reefs for 40 replicate model runs.

5.6 Local-scale effects of enhanced thermal tolerance of corals

The Reefwide analyses above indicated that outplanting of coral juveniles with enhanced thermal tolerance as a single intervention produces an only marginal increase in coral cover and condition. We examined this intervention further within the Cairns sector using ReefMod, which explicitly simulates the outplanting of individual corals over the selected reef habitats. We summarise results here and refer to Appendix B for detailed analyses. Briefly, coral outplanting was modelled as the addition of 2cm diameter coral juveniles of plating and corymbose Acropora on a reef grid (400m^2). Corals were deployed once a year from 2025 onwards in every year until 2070. We here present results of simulations for the highest density: one coral juvenile per square metre. The genotype of deployed corals was created from the local pool of genes so that genetic diversity among the outplanted specimens reflected that of the native population. To simulate the outplanting of corals with increasing thermal tolerance, the thermal optimum of each outplanted coral was elevated to target levels (e.g. +1°C or +2°C) without affecting the breadth of thermal tolerance range or the transmission of traits to future generations (i.e. heritability).

We show results here for such outplanting on 20 reefs out of the 156 reefs in the Cairns sector. Simulations assumed continual annual production of between 20 and 80 million coral juveniles with added thermal tolerance. Further, we used the most connected reefs (informed by eReefs) in the analysis, assuming this would maximise the likelihood of spreading thermal tolerance throughout the network. Finally, we implemented the condition that if a restored reef achieves 20 percent coral cover at any time step, outplanting on this reef is stopped and moved to the next source reef downstream in the network.

Results showed that increasing the optimum temperature of coral outplants by 1°C (Figure 22B) or 2°C (Figure 22C) only marginally improved reef condition in the region, while adding coral outplants with unchanged thermal tolerance (Figure 22A) resulted in no difference in reef condition. The simulated densities were unable to change the composition of thermal traits across the region, despite a focus on the most connected reefs. One explanation could be that self-recruitment, or the local growth of thermally tolerant corals, as currently parameterised in ReefMod, overrides external supply on those reefs. Detailed analyses in CoCoNet found that continuing to target any reef for more than a few years made no difference as the latest outplanting was always insignificant compared with the population established over the previous few years. Another explanation is that selecting reefs with many dispersal routes could dilute the genetic pool of larvae with enhanced thermal tolerance; in this case, a more efficient strategy might be the selection of priority reefs that have fewer (yet strategic) connections to reefs that receive larvae (I.e. sink reefs). Finally, because the outplanted (as well as native) corals have a relatively narrow temperature niche, deploying corals with 1-2°C added thermal tolerance (as a simple positive optimum shift) means that increased survival in warm summer months could be negated by slower growth and reduced fecundity at temperatures that are suboptimal for warm-adapted corals (Howells et al. 2013). These results highlight the intrinsic benefits of protecting existing coral real estate as opposed to the logistically arduous task of attempting to restore it with warm-adapted corals. Importantly, however, these analyses may underestimate the decline in coral larval supply after mass mortality. If so, then this circumstance would likely increase the efficacy of coral outplanting.

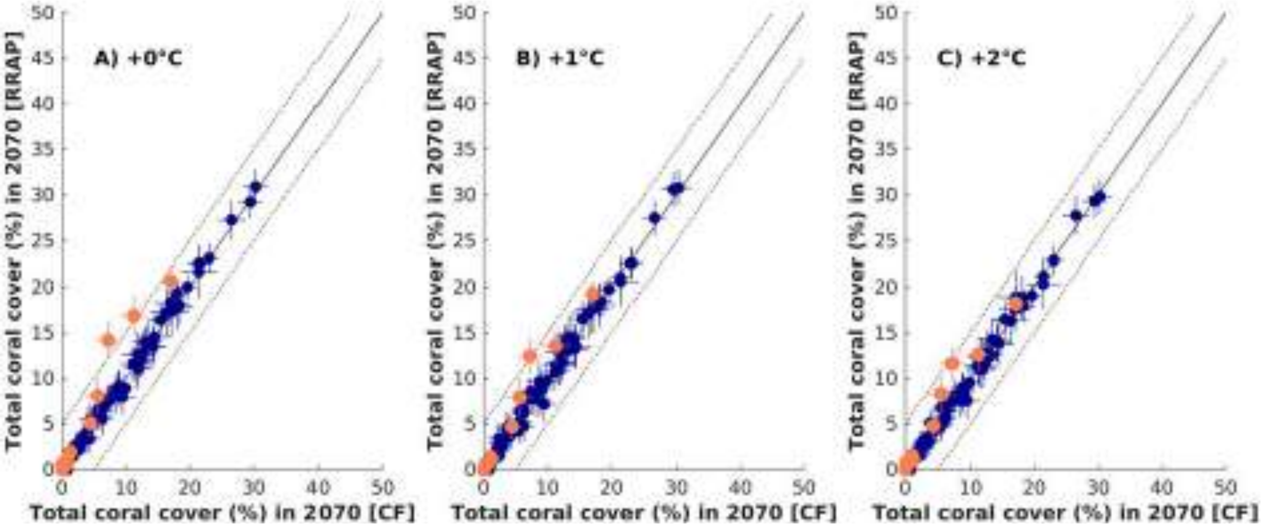


Figure 22: Effects of outplanting ~ 40 million coral juveniles with added thermal tolerance per year on 20 reefs in the Cairns region (ReefMod) under RCP 2.6 (see Appendix B2 for simulation results under RCP 8.5). Orange circle indicate reefs that were selected at least once for coral deployment. Figure: Effects of the simulated deployment is presented as change in total coral cover on the y-axis (intervention, RRAP) for the 156 reefs (circles) against that expected without intervention on the x-axis (counterfactual, CF). Results are for ReefMod in the Cairns section. Vertical and horizontal error bars are standard deviations of the mean for individual reefs for 40 replicate model runs. Results are showing (A) addition of juveniles with no added thermal tolerance and (B) with 1°C and (C) 2°C added thermal tolerance.

5.7 Probabilistic analysis of summary results

These results raise the question: what is the likelihood that interventions can deliver against RRAP objectives? We present an analysis here to inform discussions around intervention performance Reef-wide, and, in turn, to inform decision analyses. We limit this analysis to CoCoNet results for the three main interventions: warm-adapted corals, solar radiation management and additional crown-of-thorns starfish control. We did not include rubble stabilisation as it was not analysed in CoCoNet in combination with other interventions.

Briefly, we used a probabilistic Bayesian Network analysis to explore the likelihood that different interventions could deliver against a simple ecological objective:(s) sustain relative coral cover above 20 percent, or 10 percent, under the two climate change scenarios in the northern and central Reef sections. Conditional likelihoods were produced for the network of results in time, space and between interventions by importing model outputs (>23,000 simulation points from CoCoNet) via a learning routine in the software package Netica (Ni et al. 2011; Nicol and Chades 2017). We used reefs as replicates in the analysis and acknowledge that this should ideally be complemented by within-reef variation from ensemble runs. The resulting Netica interface was used to systematically explore the likelihood that a strategy (single intervention or combination) can deliver against the ecological objective at different time points and under different climate change scenarios.

We summarise results as follows. Estimated likelihoods of sustaining relative coral cover on reefs above 20 percent in the Cairns and central sectors only exceeded 50 percent under RCP 2.6 for strategies involving solar radiation management (Table 4). We note that 20 percent cover represents a higher-than-average level for the Cairns and central sections for the past decade (De'ath et al. 2012; Australian Institute of Marine Science 2017). Under RCP 2.6, the likelihood of meeting the objective of >20 percent coral cover by 2050 increased stepwise above the counterfactual from enhanced corals to the enhanced coral/solar radiation management/no crown-of-thorns starfish outbreaks solar radiation management combination in Table 4. Relaxing the objective to 10 percent coral cover under RCP 2.6 led to a higher likelihood of meeting that objective; specifically, more than 50 percent chance of meeting the objective by 2075 (Table 4).

Under RCP 8.5, these intervention combinations are only likely to sustain high coral cover (>20 percent) until the middle of the century, after which likelihoods drop to two to 15 percent. Lowering the objective to 10 percent cover increases performance likelihoods by around 20 percent. The chance of sustaining >10 percent coral cover under RCP 8.5 was only better than 50 percent for strategies involving solar radiation management, and only until 2050. The likelihood of meeting this objective was three times higher for the enhanced coral/solar radiation management/no crown-of-thorns starfish outbreaks combination compared with the counterfactual by 2050, and four to five times higher by 2075.

Table 4: Summary of likelihoods that the objective of sustaining coral cover >20 percent, or 10 percent, can be achieved with different intervention strategies under different climate scenarios. Data are conditional likelihoods (as percentages) analysed in the Netica software, based on simulated projections of coral cover for the Cairns and central regions using CoCoNet. EnC: enhanced corals, CS: cooling and shading, NCO: no crown-of-thorns starfish outbreaks.

RCP	Interventions			P (Cover >0.20)		P (Cover >0.10)	
				2050	2075	2050	2075
2.6		Counterfactual		25	19	37	27
2.6	EnC			34	30	45	43
2.6		NCO		37	44	46	54
2.6			CS	41	47	62	55
2.6	EnC	NCO		41	44	54	56
2.6	EnC		CS	53	46	62	55
2.6		NCO	CS	74	90	80	91
2.6	EnC	NCO	CS	79	91	84	92
8.5		Counterfactual		13	1	21	1
8.5	EnC			13	1	22	1
8.5		NCO		14	1	24	1
8.5			CS	39	2	49	3
8.5	EnC	NCO		16	1	26	2
8.5	HC		CS	42	3	53	9
8.5		NCO	CS	56	4	67	11
8.5	EnC	NCO	CS	66	15	74	29

6. CONCLUSIONS

We show that an example set of four RRAP interventions operating at regional to Reefwide scale have varying scope to improve the outlook for Reef coral condition until 2075. The extent to which this can be realised depends strongly on what climate change scenario unfolds. Under RCP 2.6, the large-scale interventions explored here (outplanting of up to a total of 900ha of warm-adapted corals, regional solar radiation management, additional crown-of-thorns starfish control and rubble stabilisation) could, in combination, improve Reef coral condition beyond what it is today. This represents a scenario of opportunity, but with a closing window. Under RCP 8.5, such a large-scale RRAP intervention strategy could produce benefits (by preventing decline and improving coral recovery) in the near-term, but with eventual precipitous decline by the end of the time horizon (2075).

The extent to which coral condition is expected to decline and recover will be contingent on the capacity for natural adaptation. Connectivity may interact with adaptation to drive spatial patterns of coral recovery. Under severe climate change (RCP 8.5), the models estimated strong coral decline throughout the modelled period, with coral cover in year 2075 likely to fall below five percent. A high capacity for natural adaptation would buy time for sustained coral condition in the coming decades under RCP 8.5, but followed by steep decline after 2050.

Results showed strong spatial variation, both for patterns of natural adaptation and impacts of interventions. If the spatial patterns ultimately prove unpredictable, then they would add to the large uncertainty of how counterfactual trajectories (as well as consequences of interventions) might play out, hence complicating the RRAP challenge. If, however, the spatial patterns are predictable, then spatial variation in reef condition under climate change can represent an opportunity for combined local- and large-scale interventions to improve or sustain coral condition on priority reefs.

Large-scale interventions simulated as deployed in combination showed greater efficacy than the sum of individual efficacies. Further, when analyses took account of the absolute rather than relative changes in coral cover in response to interventions, then the seemingly ineffective single intervention of outplanting warm-adapted corals added to the performance of intervention combinations. These findings are at the core of the premise of supporting ecosystem resilience under climate change (Anthony et al. 2015; McLeod et al. 2019): helping multiple processes by reducing pressures (here via solar radiation management and added crown-of-thorns starfish control), promoting processes that build resistance (warm-adapted corals) and facilitating recruitment (targeting key source and sink reefs and stabilising rubble).

At the local scale, the efficacy of rubble stabilisation depended on the ecological (benthic reef composition) and environmental (bathymetry, hydrodynamics) conditions on individual reefs. While rubble stabilisation generally showed low efficacy, its scope may be enhanced when combined with regional RRAP strategies, and in efforts to sustain priority reefs.

Finally, this study only analysed potential benefits of interventions and did not formally model risks. Also, by excluding ocean acidification from the study, projections of coral cover were likely overestimated for both the counterfactuals and simulated intervention strategies. Further, by only modelling coral cover and minimalistic estimates of composition (fast and slow-growing corals only), the potential loss of sensitive coral species and potential transitions to less species-rich coral communities were not captured in analyses.

In conclusion, modelling results presented here indicate significant scope for RRAP interventions to improve coral trajectories on the Reef. There are large uncertainties, however, pertaining to environmental and ecological drivers, the interaction with pressures not explicitly considered here (such as acidification or increasing human use of the area), to the mechanisms by which interventions will operate, and to risks of unintended consequences. We note that these uncertainties must be considered in the interpretation of results.

6.1 Model assumptions and limitations

CoCoNet and ReefMod are among the most sophisticated simulation models currently available for the Great Barrier Reef, and, like any other model, they rely on simplifying assumptions that have important implications when interpreting simulation results. The key assumptions supporting each model are summarised below (Table 5). Many of these simplifications are inherent to knowledge gaps around the biology of corals and limitations in our ability to project environmental forcing at different time and spatial scales. Consequently, our simulations should not be considered as quantitative predictions of coral cover on a specific reef, but rather as *projections* of coral condition *relative* to trajectories that the reefs could undertake in the future. Because there is a large uncertainty around the future rate of warming and the scope for coral adaptation, we considered a range of reef futures to establish plausible baseline trajectories against which the impacts of intervention can be measured. While we recognise that other baseline scenarios could be considered, a strength of our approach is to combine two ecosystem models that are structurally different yet able to each draw realistic reef projections. In doing so, we extend the range of plausible reef futures, whether they reflect different stress regimes, different assumptions regarding a specific mechanism, or different model formulations and choices. Because simulation models are key to assessing the feasibility and potential impact of Reef interventions, the RRAP R&D Program will refine some of the modelled processes and environmental forcing as more data become available. Moreover, other scenarios of reef future will be considered, with the aim of producing an ensemble of model projections able to capture a realistic envelope of uncertainty around the potential benefits of each intervention.

Table 5: Summary of assumptions used for the two ecological models (ReefMod and CoCoNet) and implications for results.

Model component	Key assumptions	Implications/limitations
Coral demographic processes	**ReefMod**: rates of coral growth, fecundity and mortality are representative of mid-depth (5-15m) forereefs. In the Cairns region, coral demographics are simulated on the reef slope habitat (3-10m depth) identified by the most recent high-resolution reef habitat mapping. Deeper populations (ie, 10-15m) are not considered as there is currently no high-resolution mapping for this habitat. **CoCoNet**: rates of coral growth, fecundity and mortality were estimated by fitting to manta tow data mainly from reef slope habitats.	Does not capture the influence of shallower (above -3m) and deeper (below -10m) coral populations (offsprings) on larval supply and export. The cost associated to coral outplanting and the stabilisation of loose rubble is representative of the restoration effort deployed on the reef slope habitat (3-10m depth) only.

Connectivity	**ReefMod**: Larval retention set to an empirical value of ~30% for all reefs as fine-scale hydrodynamics are not captured by the dispersion model. **CoCoNet:** Larval retention and exchanges are stochastic, with mean values calibrated by comparing resultant coral cover from the AIMS Long-term Monitoring Program.	Does not capture geographic (among reefs) differences in the potential of self-replenishment.
Connectivity	**ReefMod/CoCoNet**: Average connectivity patterns remain unchanged over the next 50 years.	Hydrodynamics of the Reef may change with changing wind patterns and sea level rise.
Cyclones	**ReefMod/CoCoNet**: Projected cyclone impacts do not depend on reef geomorphology and wave exposure.	ReefMod does not capture the patchiness of cyclone damages and CoCoNet does not explicitly account for variable levels of exposure across a reef. Projections may be pessimistic for habitats not exposed to storm-induced waves (e.g. leeward habitats).
Bleaching	**ReefMod**: Future climatology (annual temperatures and degree heating weeks) predicted by the HadGEM2-ES climate model for only two scenarios: RCP 2.6 and RCP 8.5. **CoCoNet**: Future climatology (degree heating weeks statistics) based on uncertain projections for only two scenarios: RCP 2.6 and RCP 8.5.	Projections depend on one climate model only. A multi-model ensemble of climate scenarios is under development, which will allow us to simulate future temperatures predicted by six climate models following four RCP scenarios (2.6, 4.5, 6.0, 8.5).
Bleaching	**ReefMod/CoCoNet**: The potential for coral growth and fecundity remains unchanged following bleaching due to a lack of empirical support for a taxon-specific parameterisation.	Projections of coral condition may be optimistic.
CoTS	**ReefMod/CoCoNet**: Population of the crown-of-thorns starfish on any reef is distributed evenly across that reef. **CoCoNet**: Distribution of crown-of-thorns starfish on any reef is not spatially resolved.	Ignores movements and aggregations within a reef, hence the patchiness of associated damages on corals.
Water quality	**ReefMod**: No link between projected storm events and projected patterns of water quality. **CoCoNet**: While storm events drive changes in water quality, the alongshore distribution of impacts is not controlled by the cyclone track.	ReefMod does not synchronise cyclone damages with storm-induced flood-plumes, whereas CoCoNet synchronises temporally but not spatially.
Water quality	**ReefMod**: assumes suspended sediments have the strongest effects on coral reproduction, growth and mortality; the effect of nutrients is not considered due to uncertain coral response. **CoCoNet**: While coral growth is lower on inshore reefs and in flood years, nutrients are not modelled explicitly.	Projections of coral condition may be optimistic on inshore reefs that are exposed to moderate to high nutrients concentrations through river plumes.
Other pressures	**ReefMod/CoCoNet**: The effects of ocean acidification are not considered due to high spatial and temporal uncertainty	Projections of coral condition may be optimistic: under high- CO_2 future (RCP 8.5), coral extension rates may be reduced while coral

		carbonate may become more susceptible to breakage from wave action; this would slow recovery rates and potentially increase damages from other disturbances (e.g. storms). Coral calcification and its impact on coral growth and mortality is being integrated within both models in relation to **eReefs** spatial predictions of water chemistry.
Other pressures	**ReefMod/CoCoNet**: the effects of coral disease are not modelled due to high spatial and temporal uncertainty.	Projections of coral condition may be optimistic, especially where the models project high coral cover.
Thermal adaptation	**ReefMod:** Present-day thermal optimums for corals are (on average) 3ºC below the maximum monthly mean temperature of reference (1985-1993 in each reef).	A 3ºC difference between coral's thermal optimums and maximum monthly mean temperature was observed at Heron Island (Marshall and Clode 2004) but may not hold across the range of latitudes covered by the entire Reef.
Thermal adaptation	**ReefMod/CoCoNet:** Bleaching susceptibility of corals is dependent on coral's thermal optimum for calcification (growth).	Bleaching and calcification might have different response curves to temperature fluctuations relative to coral's thermal optimums.
Thermal adaptation	**ReefMod/CoCoNet:** Thermal traits within a population are assumed to be representative of a single habitat (3-10m forereef).	Does not capture the influence of shallower (above -3m) and deeper (below -10m) populations on genetic adaptation.
Thermal adaptation	**ReefMod:** Coral populations on a reef are modelled by a representative 20m x 20m area; the local diversity of genotypes is simulated by imposing a rate of genetic mutations proportional to the actual reef area. **CoCoNet**: Genetic diversity is not modelled.	Genetic diversity likely underestimated. Work is ongoing to compare rates of genetic adaption using a different model where actual population sizes are considered.
Thermal adaptation	**ReefMod/CoCoNet:** all corals have the same thermal tolerance and trait heritability in the absence of empirical support for a taxon-specific parametrisation.	All corals have the same potential for thermal adaptation. Future lab experiments to inform about species-specific thermal tolerance.
Fish	**ReefMod/CoCoNet:** Herbivory is fully efficient on all reefs so that reef algae are maintained in a cropped state.	Persistent macroalgal blooms reported on some inshore reefs are not captured. Future developments for **ReefMod** to include geographic variations in fish grazing and algal productivity (informed by **eReefs**).
Cooling and shading	**ReefMod/CoCoNet**: bleaching estimated from projected reductions in seawater temperature.	The benefits of cooling and shading are probably underestimated as reductions in light intensity are not considered.

REFERENCES

Aitken SN, Whitlock MC (2013) Assisted Gene Flow to Facilitate Local Adaptation to Climate Change. Annu Rev Ecol Evol Syst 44:367–388

Albright R, Anthony KRN, Baird M, Beeden R, Byrne M, Collier C, Dove S, Fabricius K, Hoegh-Guldberg O, Kelly RP, Lough J, Mongin M, Munday PL, Pears RJ, Russell BD, Tilbrook B, Abal E (2016) Ocean acidification: Linking science to management solutions using the Great Barrier Reef as a case study. J Environ Manage 182:641–650

Anthony K, Bay LK, Costanza R, Firn J, Gunn J, Harrison P, Heyward A, Lundgren P, Mead D, Moore T, Mumby PJ, Oppen MJ van, Robertson J, Runge MC, Suggett DJ, Schaffelke B, Wachenfeld D, Walshe T (2017) New Interventions Are Needed to Save Coral Reefs. Nat Ecol Evol 1:1420–1422

Anthony KRN (2016a) Coral reefs under climate change and ocean acidification - challenges and opportunities for management and policy. Annu Rev Environ Resour 41:59–81

Anthony KRN (2016b) Coral Reefs Under Climate Change and Ocean Acidification: Challenges and Opportunities for Management and Policy. Annu Rev Environ Resour 41:1–923

Anthony KRN, Diaz-Pulido G, Verlinden N, Tilbrook B, Andersson AJ (2013) Benthic buffers and boosters of ocean acidification on coral reefs. Biogeosciences 10:4897–4909

Anthony KRN, Marshall PA, Abdulla A, Beeden R, Bergh C, Black R, Eakin CM, Game ET, Gooch M, Graham NAJ, Green A, Heron SF, van Hooidonk R, Knowland C, Mangubhai S, Marshall N, Maynard JA, Mcginnity P, Mcleod E, Mumby PJ, Nystrom M, Obura D, Oliver J, Possingham HP, Pressey RL, Rowlands GP, Tamelander J, Wachenfeld D, Wear S (2015) Operationalizing resilience for adaptive coral reef management under global environmental change. Glob Chang Biol 21:48–61

Australian Institute of Marine Science (2017) Long-term Reef Monitoring Program - Annual summary report on coral reef condition for 2016/17.

Barrett S, Lenton TM, Millner A, Tavoni A, Carpenter S, Anderies JM, Iii FSC, Crépin A, Daily G, Ehrlich P, Folke C, Galaz V, Hughes T, Kautsky N, Lambin EF, Naylor R, Nyborg K, Polasky S, Scheffer M, Wilen J, Xepapadeas A, Zeeuw A De (2014) Climate engineering reconsidered. Nat Clim Chang 4:527–529

Berkelmans R, van Oppen MJH (2006) The role of zooxanthellae in the thermal tolerance of corals: a “nugget of hope” for coral reefs in an era of climate change. Proc R Soc B-Biological Sci 273:2305–2312

Biggs BC (2013) Harnessing Natural Recovery Processes to Improve Restoration Outcomes : An Experimental Assessment of Sponge-Mediated Coral Reef Restoration. 8:

Bohensky E, Butler JRA, Costanza R, Bohnet I, Delisle A, Fabricius K, Gooch M, Kubiszewski I, Lukacs G, Pert P, Wolanski E (2011) Future makers or future takers? A scenario analysis of climate change and the Great Barrier Reef. Glob Environ Chang 21:876–893

Bozec Y-M, Mumby PJ (2014) Synergistic impacts of global warming on the resilience of coral reefs. Philos Trans R Soc B Biol Sci 370:20130267

Bozec YM, Alvarez-Filip L, Mumby PJ (2015) The dynamics of architectural complexity on coral reefs under climate change. Glob Chang Biol 21:223–235

Brodie JE, Lewis SE, Collier CJ, Wooldridge S, Bainbridge ZT, Waterhouse J, Rasheed MA, Honchin C, Holmes G, Fabricius K (2017) Setting ecologically relevant targets for river pollutant loads to meet marine water quality requirements for the Great Barrier Reef, Australia: A preliminary methodology and analysis. Ocean Coast Manag 143:136–147

Cheal AJ, MacNeil MA, Emslie MJ, Sweatman H (2017) The threat to coral reefs from more intense cyclones under climate change. Glob Chang Biol 23:1511–1524

Condie S, Condie R (2016) Retention of plankton within ocean eddies. Glob Ecol Biogeogr 25:1264–1277

Condie SA, Plagányi ÉE, Morello EB, Hock K, Beeden R (2018) Great Barrier Reef recovery through multiple interventions. Conserv Biol 32:1356–1367

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. Proc Natl Acad Sci U S A 109:17995–9

Doney SC, Fabry VJ, Feely RA, Kleypas JA (2009) Ocean Acidification: The Other CO $_2$ Problem. Ann Rev Mar Sci 1:169–192

Eakin CM, Lough JM, Heron SF (2009) Climate, weather and coral bleaching. In: van Oppen M.J.H., Lough J.M. (eds) Coral Bleaching: Patterns, Processes, Causes and Consequences. Springer, pp 41–67

Emslie MJ, Cheal AJ, Johns KA (2014) Retention of habitat complexity minimizes disassembly of reef fish communities following disturbance: a large-scale natural experiment. PLoS One 9:e105384

Fabricius KE, De'Ath G, Puotinen M, Done TJ, Cooper TF, Burgess SC (2008) Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. Limnol Ocean 53:690–704

Fisher R, Leary RAO, Low-choy S, Mengersen K, Knowlton N, Brainard RE, Caley MJ (2015) Species richness on coral reefs and the pursuit of convergent global estimates. Curr Biol 25:500–505

Fox HE, Caldwell RE (2006) Recovery from blast fishing on coral reefs: a tale of two scales. Ecol Appl 16:1631–1635

Frieler K, Meinshausen M, Golly a., Mengel M, Lebek K, Donner SD, Hoegh-Guldberg O (2012) Limiting global warming to 2 °C is unlikely to save most coral reefs. Nat Clim Chang 2:1–6

Game ET, McDonald-Madden EVE, Puotinen ML, Possingham HP (2008) Should we protect the strong or the weak? Risk, resilience, and the selection of marine protected areas. Conserv Biol 22:1619–1629

Game ET, Meijard E, Shell D, McDonald-Madden E (2014) Conservation in a wicked complex world; challenges and solutions. Conserv Lett 7:271–277

Gattuso J, Magnan AK, Bopp L, Cheung WWL, Duarte CM, Hinkel J, Mcleod E (2018) Ocean Solutions to Address Climate Change and Its Effects on Marine Ecosystems. Front Mar Sci 5:1–18

GBRMPA (2013) Great Barrier Reef Biodiversity Conservation Strategy 2013. Great Barrier Reef Marine Park Authority, Townsville

Herzfeld M, Andrewartha J, Baird M, Brinkman R, Furnas M, Gillibrand P, Hemer M, Joehnk K, Jones E, McKinnon, D., Margvelashvili, N., Mongin M, Oke P, Rizwi F, Robson B, Seaton S, Skerratt J, Tonin H, Wild-Allen K (2016) eReefs Marine Modelling: Final Report.

Hock K, Wolff NH, Beeden R, Hoey J, Condie SA, Anthony KRN, Possingham HP, Mumby PJ (2016) Controlling range expansion in habitat networks by adaptively targeting source populations. Conserv Biol 30:

Hock K, Wolff NH, Condie SA, Anthony KRN, Mumby PJ (2014) Connectivity networks reveal outbreak patterns in Crown-of-Thorns Starfish on the Great Barrier Reef. J Appl Ecol 51:1188–1196

Hock K, Wolff NH, Ortiz JC, Condie SA, Anthony KRN, Blackwell PG, Mumby PJ (2017) Connectivity and systemic resilience of the Great Barrier Reef. PLoS Biol 15:e2003355

Hoegh-Guldberg O, Hughes L, McIntyre S, Lindenmayer DB, Parmesan C, Possingham HP, Thomas CD (2008) Assisted colonization and rapid climate change. Science 321:345–346

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Stenack RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Inglesias-Priesto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral Reefs Under Rapid Climate Change and Ocean Acidification. Science (80-) 318:1737–1742

Howells EJ, Beltran VH, Larsen NW, Bay LK, Willis BL, van Oppen MJH (2011) Coral thermal tolerance shaped by local adaptation of photosymbionts. Nat Clim Chang 2:116–120

Howells EJ, Berkelmans R, Van Oppen MJH, Willis BL, Bay LK (2013) Historical thermal regimes define limits to coral acclimatization. Ecology 94:1078–1088

Hughes TP (1999) Off-reef transport of coral fragments at Lizard Island, Australia. Mar Geol 157:1–6

Hughes TP, Kerry JT, Baird AH, Connolly SR, Dietzel A, Eakin CM, Heron SF, Hoey AS, Hoogenboom MO, Liu G, McWilliam MJ, Pears RJ, Pratchett MS, Skirving WJ, Stella JS, Torda G (2018) Global warming transforms coral reef assemblages. Nature 556:492

IPCC (2014) Climate Change 2014: Synthesis Report. Contribution of Working Groups I, II and III to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change. IPCC, Geneva, Switzerland

King AD, Karoly DJ, Henley BJ (2017) Australian climate extremes at 1.5°C and 2°C of global warming. Nat Clim Chang 7:412–416

Knutti R, Joos F, Müller SA, Plattner GK, Stocker TF (2005) Probabilistic climate change projections for CO_2 stabilization profiles. Geophys Res Lett 32:1–4

Lesser MP, Farrell JH (2004) Exposure to solar radiation increases damage to both host tissues and algal symbionts of corals during thermal stress. Coral Reefs 23:267–377

Logan CA, Dunne JP, Eakin CM, Donner SD (2014) Incorporating adaptive responses into future projections of coral bleaching. Glob Chang Biol 20:125–139

Lough JM, Anderson KD, Hughes TP (2018) Increasing thermal stress for tropical coral reefs: 1871–2017. Sci Rep 8:6079

MacNeil MA, Mellin C, Pratchett MS, Hoey J, Anthony KRN, Cheal AJ, Miller I, Sweatman H, Cowan ZL, Taylor S, Moon S, Fonnesbeck CJ (2016) Joint estimation of crown of thorns (*Acanthaster planci*) densities on the Great Barrier Reef. PeerJ 4:e2310

Matthews HD, Caldeira K (2007) Transient climate – carbon simulations of planetary geoengineering. Proc Natl Acad Sci US 104:9949–9954

Matz M V., Treml EA, Aglyamova G V., Bay LK (2018) Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. PLoS Genet 14:1–19

Maynard JA, Anthony KRN, Marshall PA, Masiri I (2008) Major bleaching events can lead to increased thermal tolerance in corals. Mar Biol 155:173–182

Mcleod E, Anthony KRN, Mumby PJ, Maynard J, Beeden R, Graham NAJ, Heron SF, Hoegh-guldberg O, Jupiter S, Macgowan P, Mangubhai S, Marshall N, Marshall PA, Mcclanahan TR, Mcleod K, Nyström M, Obura D, Parker B, Possingham HP, Salm R V, Tamelander J (2019) The future of resilience-based management in coral reef ecosystems. J Environ Manage 233:291–301

Mongin M, Baird ME, Tilbrook B, Matear RJ, Lenton A, Herzfeld M, Wild-allen K, Skerratt J, Margvelashvili N, Robson BJ, Duarte CM, Gustafsson MSM, Ralph PJ, Steven ADL (2016) The exposure of the Great Barrier Reef to ocean acidification. Nat Commun 7:1–8

Morello EB, Plagányi ÉE, Babcock RC, Sweatman H, Hillary R, Punt AE (2014) Model to manage and reduce crown-of-thorns starfish outbreaks. 512:167–183

Mumby PJ, Chisholm SW, Edwards AJ, Andrefouet S, Jaubert J (2001) Cloudy weather may have saved Society Island reef corals during the 1998 ENSO event. Mar Ecol Prog Ser 222:209–216

Mumby PJ, Hastings A, Edwards HJ (2007) Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101

NASEM (2018) A Research Review of Interventions to Increase the Persistence and Resilience of Coral Reefs. Natl Acad Sci Eng Med https//doi.org/1017226/25279

Ni Z, Phillips LD, Hanna GB (2011) Exploring Bayesian Belief Networks Using Netica. In: Athanasiou T., Darzi A. (eds) Evidence Synthesis in Healthcare. Springer Verlag, London, pp

293–318

Nicol S, Chades I (2017) A preliminary approach to quantifying the overall environmental risks posed by development projects during environmental impact assessment. PLOSone 12: e01809:1–21

van Oppen MJH, Gates RD, Blackall LL, Cantin N, Chakravarti LJ, Chan WY, Cormick C, Crean A, Damjanovic K, Epstein H, Harrison PL, Jones T., Miller M, Pears RJ, Peplow LM, Raftos DA, Schaffelke B, K S, Torda G, Wachenfeld D, Weeks AR, Putnam HM (2017) Shifting paradigms in restoration of the world's coral reefs. Glob Chang Biol 23:3437–3448

van Oppen MJH, Oliver JK, Putnam HM, Gates RD (2015) Building coral reef resilience through assisted evolution. Proc Natl Acad Sci 112:1–7

Ortiz JC, Bozec Y-M, Wolff NH, Doropoulos C, Mumby PJ (2014) Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. Nat Clim Chang 4:1090–1094

Possingham HP, Andelman SJ, Noon BR, Trombulak S, Pulliam HR (2001) Making smart conservation decisions. In: Orians G., Soule´ M. (eds) Research priorities for conservation biology. Island Press, California,

Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of Crown of Thorns Starfish (Acanthaster spp). Oceanogr Mar Biol an Annu Rev 52:133–200

Puotinen M, Maynard JA, Beeden R, Radford B, Williams GJ (2016) A robust operational model for predicting where tropical cyclone waves damage coral reefs. Sci Rep 6:26009

Puotinen ML (2007) Modelling the risk of cyclone wave damage to coral reefs using GIS: a case study of the Great Barrier Reef, 1969,Äì2003. Int J Geogr Inf Sci 21:97–120

Ricciardi A, Simberloff D (2009) Assisted colonization is not a viable conservation strategy. Trends Ecol Evol 24:248–253

Richards ZT (2013) A comparison of proxy performance in coral biodiversity monitoring. Coral Reefs 32:287–292

Rivera-Posada J, Owens L, Caballes CF, Pratchett MS (2012) The role of protein extracts in the induction of disease in Acanthaster planci. J Exp Mar Bio Ecol 429:1–6

Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. Curr Biol 24:1000–1005

Rosa IMD, Pereira HM, Ferrier S, Alkemade R, Acosta LA, Akcakaya R, Belder E, Fazel AM, Fujimori S, Harfoot M, Harhash KA, Harrison PA, Hauck J, Hendriks RJJ, Hernández G, Jetz W, Karlsson-vinkhuyzen SI, Kim H, King N, Kok MTJ, Kolomytsev GO, Lazarova T, Leadley P, Lundquist CJ, Márquez JG, Meyer C, Navarro LM, Nesshöver C, Ngo HT, Ninan KN, Palomo MG, Pereira LM, Peterson GD, Pichs R, Popp A, Purvis A, Ravera F, Rondinini C, Sathyapalan J, Schipper AM (2017) Multiscale scenarios for nature futures. Nat Ecol Evol

Roth C, Addison J, Anthony K, Dale A, Eberhard R, Hobday A, Jarvis D, Kroon F, Stone-jovicich

S, Walshe T (2017) Reef 2050 Plan Review Options. Final Report submitted to the Department of the Environment and Energy.

Sampayo EM, Ridgway T, Bongaerts P, Hoegh-Guldberg O (2008) Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proc Natl Acad Sci U S A 105:10444–10449

Skirving W, Enríquez S, Hedley JD, Dove S, Eakin CM, Mason RAB, Cour JLD La, Liu G, Hoegh-Guldberg O, Strong AE, Mumby PJ, Iglesias-Prieto R (2018) Remote sensing of coral bleaching using temperature and light: Progress towards an operational algorithm. Remote Sens 10:18

Thornton PK, Ericksen PJ, Herrero M, Challinor AJ (2014) Climate variability and vulnerability to climate change: a review. Glob Chang Biol 20:3313–3328

Trenberth KE, Fasullo JT, Shepherd TG (2015) Attribution of climate extreme events. Nat Clim Chang 5:725–730

Vercelloni J, Clifford S, Caley MJ, Pearse AR, Brown R, James A, Christensen B, Bednarz T, Anthony K, González-rivero M, Mengersen K, Peterson EE (2018) Using virtual reality to estimate aesthetic values of coral reefs. R Soc Open Sci 5:172226

Veron JEN (2000) Corals of the World. Australian Institute of Marine Science,

Wallace CC (1999) Staghorn Corals of the World: a revision of the coral genus Acropora. CSIRO Publishing, Collingwood

Walshe T, Anthony K (2017) Towards Solving the Crown-of-Thorns Starfish Problem on the Great Barrier Reef Accelerate Prepared by.

Westcott DA, Fletcher CS, Babcock R, Plaganyi-Lloyd E (2016) A Strategy to Link Research and Management of Crown-of-Thorns Starfish on the Great Barrier Reef: An Integrated Pest Management Approach. Final report to the National Environmental Research Programme.

Woesik R van, Golbuu Y, Roff G (2015) Keep up or drown: adjustment of western Pacific coral reefs to sea-level rise in the 21st century. R Soc Open Sci 2:150181

Van Woesik R, Sakai K, Ganase A, Loya Y (2011) Revisiting the winners and the losers a decade after coral bleaching. Mar Ecol Prog Ser 434:67–76

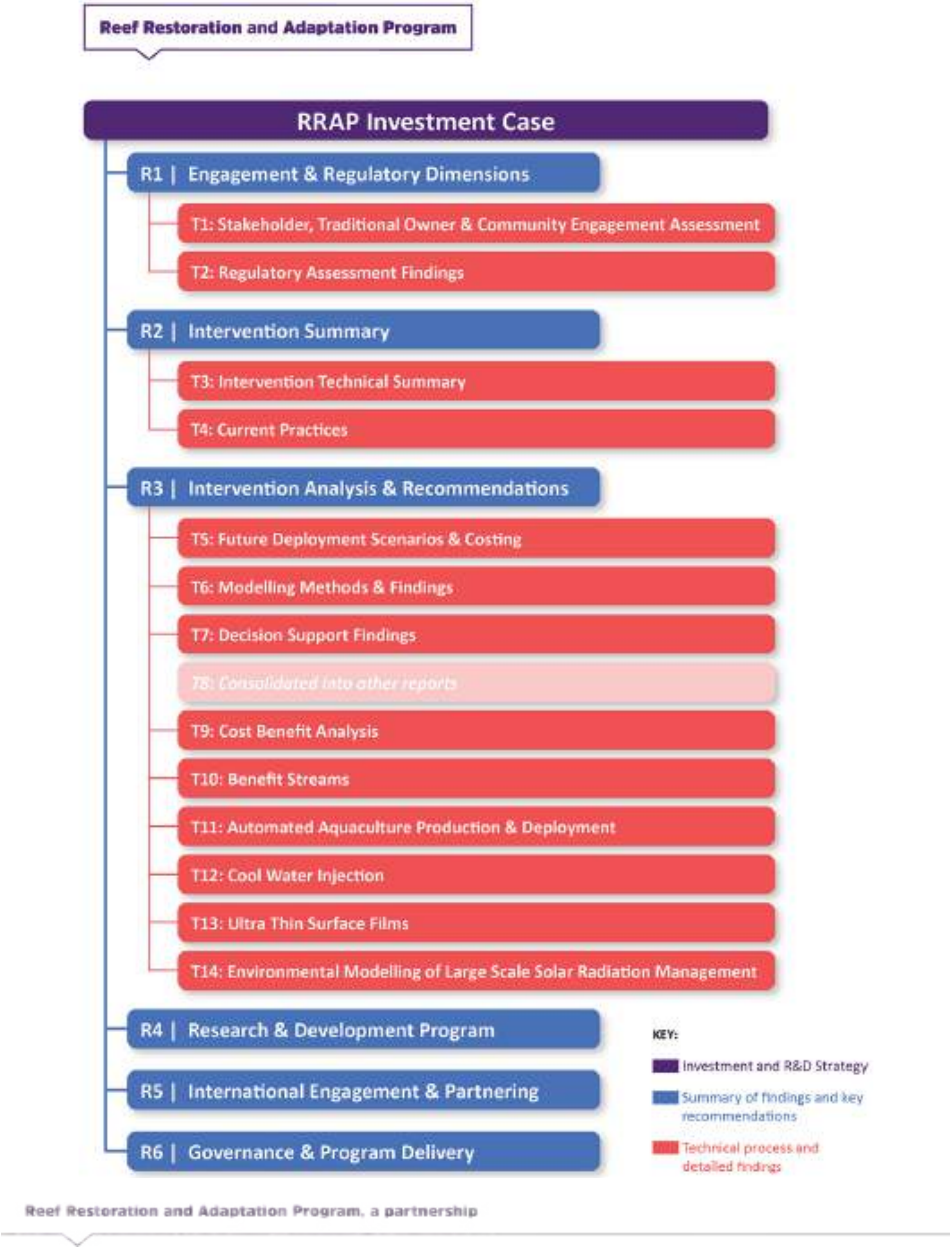
Wolff NH, Donner SD, Cao L, Iglesias-Prieto R, Sale PF, Mumby PJ (2015) Global inequities between polluters and the polluted: Climate change impacts on coral reefs. Glob Chang Biol 21:3982–3994

Wolff NH, Mumby PJ, Devlin M, Anthony KRN (2018a) Vulnerability of the Great Barrier Reef to climate change and local pressures. Glob Chang Biol 24:1978–1991

Wolff NH, da Silva ET, Devlin M, Anthony KRN, Lewis S, Tonin H, Brinkman R, Mumby PJ (2018b) Contribution of individual rivers to Great Barrier Reef nitrogen exposure with implications for management prioritization. Mar Pollut Bull 133:30–43

Wolff NH, Wong A, Vitolo R, Stolberg K, Anthony KRN, Mumby PJ (2016) Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs 35:613–623

APPENDIX A – RRAP DOCUMENT MAP



Reef Restoration and Adaptation Program

RRAP Investment Case

- **R1 | Engagement & Regulatory Dimensions**
  - T1: Stakeholder, Traditional Owner & Community Engagement Assessment
  - T2: Regulatory Assessment Findings
- **R2 | Intervention Summary**
  - T3: Intervention Technical Summary
  - T4: Current Practices
- **R3 | Intervention Analysis & Recommendations**
  - T5: Future Deployment Scenarios & Costing
  - T6: Modelling Methods & Findings
  - T7: Decision Support Findings
  - *T8: Consolidated into other reports*
  - T9: Cost Benefit Analysis
  - T10: Benefit Streams
  - T11: Automated Aquaculture Production & Deployment
  - T12: Cool Water Injection
  - T13: Ultra Thin Surface Films
  - T14: Environmental Modelling of Large Scale Solar Radiation Management
- **R4 | Research & Development Program**
- **R5 | International Engagement & Partnering**
- **R6 | Governance & Program Delivery**

KEY:

🟪 Investment and R&D Strategy

🟦 Summary of findings and key recommendations

🟥 Technical process and detailed findings

Reef Restoration and Adaptation Program, a partnership

APPENDIX B1 – DETAILED DESCRIPTION OF THE COCONET MODEL

Scott Condie, CSIRO

The Coral and Crown-of-thorns starfish Network (CoCoNet) meta-community model has been described previously (Condie et al. 2018b), including calibration against data from the Australian Institute of Marine Sciences (AIMS) Long-term Monitoring Program and parameter sensitivity analyses. It consists of a dynamic network of individual reefs connected through larval recruitment of corals and crown-of-thorns starfish. The most recent implementation uses a network of 2096 reefs, corresponding to the size and location of the 2096 largest reefs within the Great Barrier Reef.

B1.1 Reef ecology

In CoCoNet, reefs support populations of fast-growing corals (e.g. *Acropora* and *Montipora* spp.) and massive slow-growing corals (e.g. *Faviidae* and *Porites* spp.); as well as their major predator, the crown-of-thorns starfish. Crown-of-thorns starfish populations were age-structured, differentiating larvae (year 0), juveniles (year 1) and adults (years 2+). Trophic interactions between corals and crown-of-thorns starfish are calculated using a model that included a preference for feeding on fast-growing coral and rate parameters (growth, predation and natural mortalities) fitted to data from the Long-term Monitoring Program (Morello et al. 2014, Plaganyi et al. 2014). Each reef has a fixed coral-carrying capacity proportional to the area of the reef.

Reef connectivity involves spawning, larval transport by ocean currents and successful settlement onto either a natal reef (self-recruitment) or neighbouring reefs (cross-recruitment). It was modelled as directed links that appeared and disappeared from year to year with exchanges that also varied stochastically to represent variability in ocean currents and larval survival. The probability of successful recruitment from one reef to another was proportional to the connectivity estimated from particle tracking experiments, although recruitment to a reef was reduced by the proportion of coral rubble previously generated by cyclone and bleaching induced coral mortality.

The structure of the reef network was estimated using ocean current patterns from the eReefs 1-km resolution hydrodynamic model (Hock et al. 2014, Condie and Condie 2016, Hock et al. 2016, Hock et al. 2017). Both coral and crown-of-thorns starfish spawning events were simulated over three years of available currents (2016-2018), which included both wet and dry extremes. Particles were released from all reefs over their respective spawning periods. Particles were advected by the current fields, with the imposition of biological constraints such as preferred swimming depths and larval mortality rates (Condie et al. 2018b). A directed link was established between two reefs when a particle released from one reef passed within 1km of another reef during the period when larvae would have been competent to settle. The 1km ‘capture halo’ allowed for any directed swimming of larvae (weak for corals and crown-of-thorns starfish) and the limited resolution of current fields that may not resolve features such as lee eddies. All directed links were combined into a 2096 x 2096 reef connectivity matrix with each element indicating the number of particle connections between two reefs. Connectivity matrices were generated for each of the three coral spawning seasons and each of the three crown-of-thorns starfish spawning seasons.

Using the connectivity matrices directly in CoCoNet would have not only restricted the choice of connectivity patterns to the three modelled spawning periods available through eReefs but have would also increase the computational cost of the model by several orders of magnitude. Instead, the median weighted in-degree centrality (product of the number of incoming connections and the average weight of those connections) was calculated for each 0.2 x 0.2 degree cell using the three years of data for both corals and crown-of-thorns starfish. A third order (cubic) polynomial surface in longitude, latitude and weighted out-degree was then fitted on the same geographic grid using linear regression. Third order polynomials were found to capture the broad-scale variations in out-degree across the Reef with much lower RMS errors than could be achieved with a second order (quadratic) polynomial.

The cubic surface provided a connectivity probability distribution for the reef network. For each spawning event, the probability of forming an incoming link to any reef increased in proportion to the connectivity probability distribution. There was also preferential linking (Dorogovtsev et al. 2000) of larger reefs to reflect their larger capture halos. This process gave the network a scale-free structure with larger reefs tending to form connectivity hubs, consistent with previous graph theory analysis of one section of the Reef (Kininmonth et al. 2010).

The final connectivity network provides relative probabilities of links forming between any two reefs. The calibration process then determined the mean number of links and mean recruitment for each coral and crown-of-thorns starfish group that aligned the modelled median and range of coral and COTS populations with observations from the Long-term Monitoring Program.

B1.2 Environmental forcing

Reefs were subjected to environmental stressors in the form of tropical cyclones and associated flooding, and coral bleaching events. These stressors changed over the simulations on the basis of climate projections. The resulting scenarios are considered plausible and consistent with published estimates. However, there are clearly large uncertainties in all of the modelled climate impacts.

B1.2.1Tropical cyclones and flood plumes

Parameterisation of tropical cyclones (including tropical lows) were represented as described previously (Condie et al. 2018a). Events were applied stochastically at frequencies and intensities consistent with recent historical conditions (Puotinen 2007, Puotinen et al. 2016, Wolff et al. 2016). Coral mortality within the spatial footprint of each cyclone event increased with the category of cyclone (1-5), with a commensurate increase in coral rubble cover.
Cyclone-induced flooding also reduced coral growth rates and increased rates of crown-of-thorns starfish recruitment. Coral growth decayed exponentially from its offshore value towards zero at the coastline (Wooldridge et al. 2006, Wenger et al. 2016), whereas crown-of-thorns starfish recruitment increased exponentially towards the coast peaking at five times the offshore value at the coastline (Fabricius et al. 2010, Wolfe et al. 2015). In both instances, the offshore e-folding scale increased by a factor of five from the northern to the southern extent of the Reef, reflecting differences in the level of human disturbance of adjacent catchments (Wooldridge et al. 2006). Throughout the Reef, the offshore scale also increased with increasing cyclone category. The maximum offshore scale was limited to 75km, consistent with the estimated influence of river flood plumes (Wolff et al. 2018).

Future projections assumed that while the overall frequency of cyclones remained unchanged, the frequency of category 5 cyclones increased by 50 percent. This value is intermediate within recently reviewed estimates (Cheal et al. 2017) that range from 15 percent (Leslie et al. 2007) to 150 percent (Walsh et al. 2004). Even with a 50 percent increase, the frequency of category 5 cyclones after 2050 remains much less than the frequency observed on the Reef over the past decade. The coral mortalities associated with different categories of cyclone were parameterised using results from post-cyclone surveys (Fabricius et al. 2008). However, these too were applied stochastically to capture the high spatial variability in mortality that is typically observed.

B1.2.2 Coral bleaching events

Similar to tropical cyclones, coral bleaching was implemented as random events dependent on exposure of reefs to high temperatures over time expressed in terms of degree heating weeks (degree heating weeks). Coral mortality within the spatial footprint of bleaching events increased with degree heating weeks, with a commensurate increase in coral rubble cover. Plausible future scenarios for maximum annual degree heating weeks were estimated from preliminary estimates of Wolff (Pers. Comm.) and extrapolations of past bleaching events (Lough et al. 2018) (Figure 23).

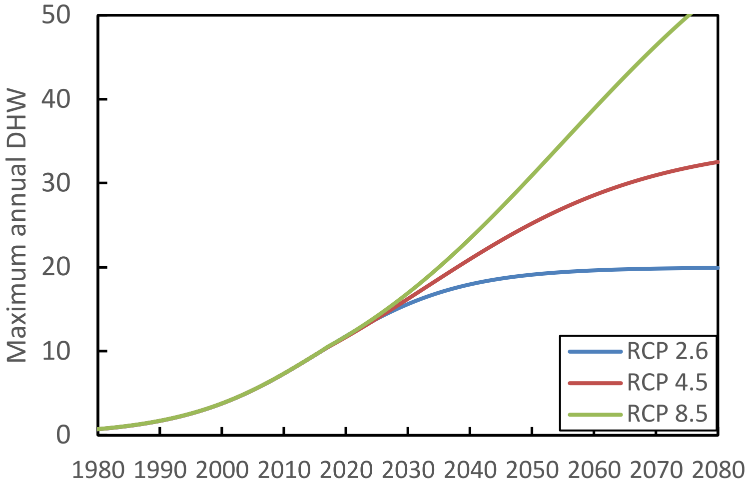


Figure 23: Maximum annual degree heating weeks used under the three RCP scenarios. Each year of a scenario, degree heating weeks were set at a level randomly selected from below the maximum annual egree heating weeks curve.

In any year, a bleaching event can occur with the maximum geographical extent of the bleaching event increasing with maximum annual degree heating weeks. The ratio of these two quantities was selected to ensure that the average proportion of locations bleached on the Reef per annum aligned with corresponding empirical estimates from the Australasian region (Figure 24) (Hughes et al. 2018).

With size and degree heating weeks distributions for bleaching events aligned with the limited available empirical data, the next step was to estimate the associated coral mortality. Maximum bleaching mortality was related to degree heating weeks using a Gompertz function fitted to data from the 2016 mass bleaching event on the Reef (Figure 25) (Hughes et al. 2017). For each bleaching event, the degree heating weeks was randomly selected from beneath the distribution in Figure 23. The mortality of each coral group was then estimated for each reef by randomly selecting from beneath the square of the distribution in Figure B1.3 (i.e. Chi-squared distribution with one degree of freedom) and taking the square root of this quantity so as to weight towards higher mortalities as suggested by observed mortality rates. The mortality curves are separated by differences in natural thermal tolerance of coral groups (measured in degree heating weeks), with slow-growing corals tending to be more thermally-tolerant than fast-growing corals (Marshall and Baird 2000).

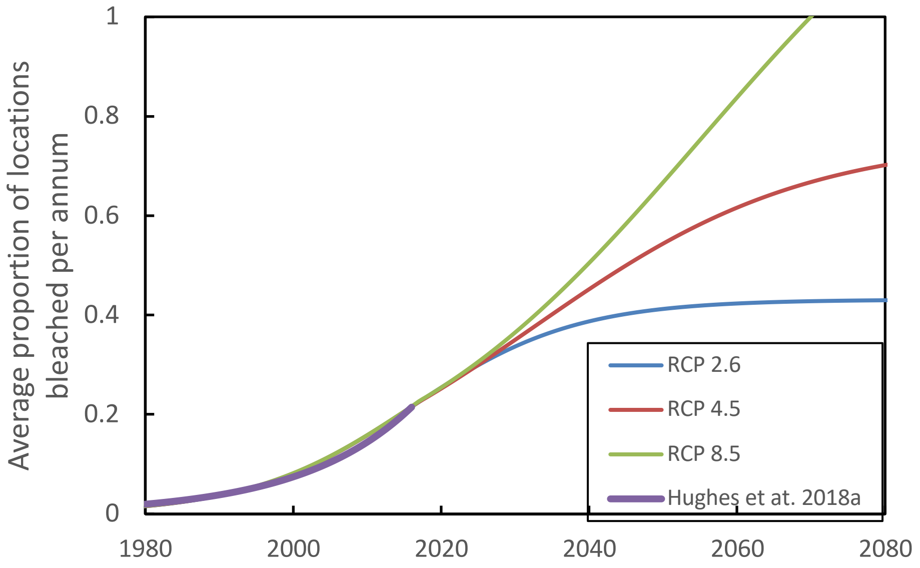


Figure 24: Average proportion of locations bleached under the three RCP scenarios and corresponding estimates from empirical data for 1980-2016 (Hughes et al. 2018). The long-term values are also consistent with the frequency of bleaching (>2 DHM) estimated from climate model projections for RCP 2.6 (0.35-0.45) and RCP 4.5 (0.55-0.75) (Frieler et al. 2013).

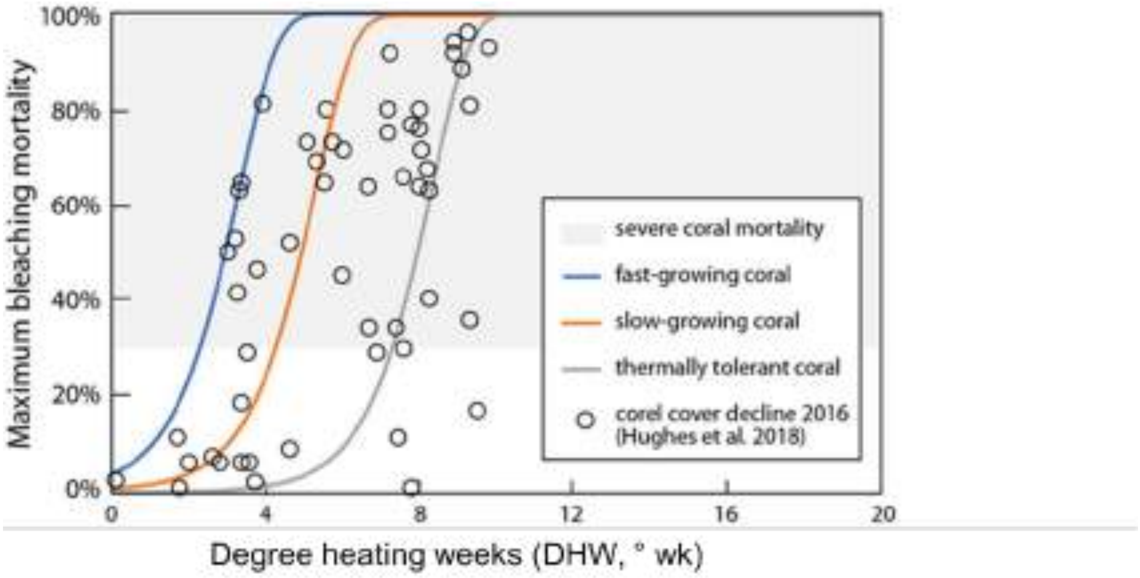


Figure 25: Maximum bleaching mortality as a function of degree heating weeks for three coral groups and observed bleaching mortalities on individual reefs following the 2016 bleaching event on the Great Barrier Reef (Hughes et al. 2018).

B1.3 Natural adaptation of corals

The thermal tolerance of any coral group can change through natural adaptation. However, there are various approaches that can be used to model this process and the rates and maximum extent of adaptation are still largely unknown. We therefore implemented a parsimonious model that captured only the essential dynamics of coral adaptation.

The rate of adaption was controlled by an adaptability score. Following each bleaching event, the thermal tolerance of surviving corals (measured in degree heating weeks) was increased by a factor of $(1+\text{adaptability})^{\sqrt{\text{mortality}}}$, so that the adaptability score controlled the rate of adaption (Figure B26). This was considered the simplest conceivable model in which thermal tolerance increased at a decreasing rate with mortality and remained unchanged if either adaptability or bleaching mortality were zero.

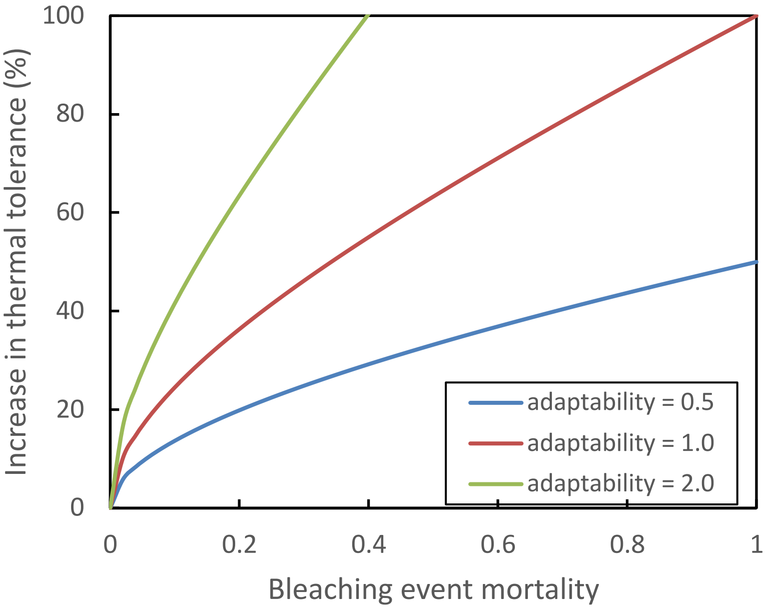


Figure 26: Percentage increase in thermal tolerance of coral surviving a bleaching event as a function of bleaching mortality. Initial thermal tolerance values were: 1 for fast-growing corals; 3 for slow-growing corals; and 6 for bleaching-resistant corals.

In the absence of continuing thermal stress, thermal tolerance gradually declined again as the community structure within each coral group recovered (Maynard et al. 2008, Sampayo et al. 2008, van Woesik et al. 2011, Logan et al. 2014) or corals shuffled their zooxanthellae populations to more thermally-tolerant symbiont types (Sampayo et al. 2008, Logan et al. 2014). The exponential timescale for decline associated with a coral group’s community structure was assumed to be inversely proportional to the growth rate of the group (10-years for fast-growing corals and 50-years for slow-growing corals) (Maynard et al. 2008, Sampayo et al. 2008, van Woesik et al. 2011, Logan et al. 2014). However, shorter timescales (two to five years) may be appropriate where corals adapt by shuffling their zooxanthellae populations (Sampayo et al. 2008, Logan et al. 2014).

The adaptive capacity of corals was also limited by imposing both a cap on the cumulative change in thermal tolerance and a growth rate penalty per degree heating weeks increase in thermal tolerance. Because the default cap was set to a relatively high value (26 degree heating weeks), the growth rate penalty (0.5 percent per degree heating weeks) was generally the main limiting factor.

Thermal tolerance was heritable in that recruitment from neighbouring reefs contributed to the average thermal tolerance of the receiving reef. However, averaging at the reef scale limited the propagation of traits, except to reefs where the existing coral cover was very low. An implicit model assumption is therefore that local adaptation in direct response to heat stress tends to be the main driver of adaptation, rather than propagation of traits from reef to reef. This assumption has not yet been tested empirically.

The net rate of adaptation in the model was largely controlled by the adaptability parameter (Figure B1.4). While adaptation rates on the Reef are largely unknown, setting adaptability to 0.5 resulted in long-term improvements in coral cover under RCP 2.6; and from around 2045, delayed coral decline by 10-15 years under RCP 8.5. These effects are broadly consistent with mid-range adaptive responses to sea surface temperature projections (Logan et al. 2014). However, representation of natural adaptation should be regarded as preliminary at this time with a more sophisticated treatment provided by ReefMod (Appendix B2).

B1.4 Interventions

Short- and long-term intervention options were identified from existing management practices, expert advice and the scientific literature. Interventions could be classified as either regional-scale or reef-scale. In the latter case, the number of reefs treated was generally limited by some form of intervention capacity. Under these circumstances, the highest priority was given to the most connected reefs (within 10 latitudinal bands evenly distributed over the full length of the Reef).

B1.4.1 Coastal catchment restoration

Quantifying the influence of catchment restoration on reef ecology is still a major challenge (Brodie et al. 2012). Implementation of catchment restoration in the model reduced the influence of floods on both coral growth and recruitment of crown-of-thorns starfish larvae. Maximum improvement in catchment condition was assumed to have an effect equivalent to reducing the intensity of tropical cyclones and lows by one cyclone category. For a category 3 cyclone, this had the effect of reducing the offshore scale of catchment influences by one third. This equates to around 42 percent of the difference between southern and far northern catchments on the Reef, which has previously been used as an indication of the maximum improvement that might be achievable through catchment restoration (Wooldridge et al. 2006). Hence, the limits placed on catchment restoration in the model were broadly consistent with geographical differences in catchment condition.

In model runs, active catchment restoration was started in 2021 and approached its final state over an e-folding timescale of 20 years.

B1.4.2 Crown-of-thorns starfish control

Implementation of crown-of-thorns starfish control in the model was closely based on the approach used by control vessels currently operating on the Reef. Each vessel operated 250 days per year, which was divided into 25 10-day voyages, with a maximum of 90 percent of this time spent on-reef. For each voyage, highly connected reefs and then other reefs were checked at random until a crown-of-thorns starfish outbreak (>0.2 crown-of-thorns starfish per manta tow) was detected. Every time a reef was checked, 0.1 days of the available voyage time was removed to capture the impact of increased transit times when outbreaks were rare.

Once an outbreak was identified, this reef was targeted along with other reefs within a radius of 6-14km (selected randomly). The detectability of adult crown-of-thorns starfish on the Reef was initially estimated to be in the range 77-87 percent (MacNeil et al. 2016). However, recent studies suggest this figure is very optimistic and a more conservative rate of 60 percent has been adopted for the simulations (Morgan Pratchett, pers. comm.). The time spent on each reef increased linearly with the area of the reef, with the average sized reef in the system consuming three days of a voyage. Each voyage ended when all 10 days had been used and the total number of voyages each year was 25 times the number of available vessels.

B1.4.3 Rubble stabilisation

Coral rubble was generated as a direct consequence of coral mortality during cyclone and bleaching events. The area of rubble cover was assumed to be twice that of the contributing live coral cover (corresponding to a hemispherical surface of live coral collapsing onto a flat seabed). Rubble cover was tracked on all reefs and decayed exponentially with a decay timescale of 5.5 years consistent with studies of natural rubble consolidation (Biggs 2013).

Additional rubble stabilisation could be implemented over a specified area and number of reefs. Each year, highly connected reefs and then other reefs were checked at random to identify either 20 or 100 reefs with low coral cover and high rubble cover. A specified area of rubble was stabilised on each of these reefs (either 5ha or 1ha, giving a total of 100ha across the Reef). This process increased rates of coral recruitment up to a maximum of 80 percent of the rate with zero rubble.

B1.4.4 Solar radiation management across the Reef

Solar radiation management was also specified in the model as a fixed reduction in degree heating weeks, but at regional or Reefwide scales. Because of the larger scale, it is expected that higher degree heating weeks reductions should be achievable.

B1.4.5 Introduction of thermally tolerant corals

The thermally tolerant coral group was characterised by lower rates of mortality during bleaching events (Figure B1.3). These corals could be seeded as larvae or outplanted as juveniles with any initial coverage. Enhanced mortality immediately following outplanting was not explicitly modelled, so that the initial coverage represented only successful outplants. This formulation can also be applied to larval seeding by factoring in the expected high mortality prior to recruitment.

Annual outplanting was undertaken on a limited number of reefs, targeted at 100 of the 500 most highly connected reefs with low existing coral cover (<20 percent). A total of either 10 or 100 million juvenile coral colonies (5cm diameter) were outplanted annually in simulations across the 100 reefs (total of 90 to 900 hectares of new, enhanced corals outplanted over the 45-year horizon simulated).

Thermally tolerant corals can represent a distinct group with no interbreeding with either fast-growing or slow-growing coral groups. Alternatively, they can represent a strain capable of interbreeding. Because each group represented many coral species, interbreeding was limited to a fixed proportion of the fast-growing or slow-growing population. Specifically, thermally tolerant corals were assumed to be capable of interbreeding with 10 percent of the fast-growing coral group (and 0 percent of the slow-growing group). Hybrids recruited to each reef were proportionally allocated to each of the two interbreeding groups, with proportionate changes in their thermal tolerance.

B1.5 Ensemble runs to test adaptation pathways

Adaptation pathways were defined in terms of the types and timing of interventions applied during each simulation. Each intervention was individually tested, and a small number were also tested as combinations. Testing covered both moderate (RCP 2.6) and extreme climate changes (RCP 8.5) as described above.

Each simulation started in 1951 and ended in 2080, with the first 30 years treated as an equilibration period. Early interventions (e.g. catchment restoration, crown-of-thorns starfish control) were started in 2021, and latter interventions (e.g. rubble stabilisation, solar radiation management, introduction of thermally tolerant corals) in 2031. The combination and timing of interventions defined the adaptation pathway to be tested.

For each adaptation pathway, simulations were repeated 50 times to form an ensemble. For each run within the ensemble, the initial coral and crown-of-thorns starfish populations were varied randomly. Environmental forcing was also varied randomly within the prescribed distributions set by the climate scenario (RCP 2.6 or RCP 8.5). This approach provided statistically representative ensembles.

Appendix B1 References

Biggs, B. C. 2013. Harnessing Natural Recovery Processes to Improve Restoration Outcomes: An Experimental Assessment of Sponge-Mediated Coral Reef Restoration. Plos One **8**.

Brodie, J. E., F. J. Kroon, B. Schaffelke, E. C. Wolanski, S. E. Lewis, M. J. Devlin, I. C. Bohnet, Z. T. Bainbridge, J. Waterhouse, and A. M. Davis. 2012. Terrestrial pollutant runoff to the Great Barrier Reef: An update of issues, priorities and management responses. Marine Pollution Bulletin **65**:81-100.

Cheal, A. J., M. A. Macneil, M. J. Emslie, and H. Sweatman. 2017. The threat to coral reefs from more intense cyclones under climate change. Global Change Biology **23**:1511-1524.

Condie, S., and R. Condie. 2016. Retention of plankton within ocean eddies. Global Ecology and Biogeography **25**:1264-1277.

Condie, S. A., E. E. Plaganyi, E. B. Morello, K. Hock, and R. Beeden. 2018a. Cumulative impacts require multiple interventions on the Great Barrier Reef. Conservation Biology.

Condie, S. A., E. E. Plaganyi, E. B. Morello, K. Hock, and R. Beeden. 2018b. Great Barrier Reef recovery through multiple interventions. Conservation Biology **32**:1356-1367.

Dorogovtsev, S. N., J. F. F. Mendes, and A. N. Samukhin. 2000. Structure of growing networks with preferential linking. Physical Review Letters **85**:4633-4636.

Fabricius, K. E., G. De'ath, M. L. Puotinen, T. Done, T. F. Cooper, and S. C. Burgess. 2008. Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. Limnology and Oceanography **53**:690-704.

Fabricius, K. E., K. Okaji, and G. De'ath. 2010. Three lines of evidence to link outbreaks of the crown-of-thorns seastar Acanthaster planci to the release of larval food limitation. Coral Reefs **29**:593-605.

Frieler, K., M. Meinshausen, A. Golly, M. Mengel, K. Lebek, S. D. Donner, and O. Hoegh-Guldberg. 2013. Limiting global warming to 2 degrees C is unlikely to save most coral reefs. Nature Climate Change **3**:165-170.

Hock, K., N. H. Wolff, R. Beeden, J. Hoey, S. A. Condie, K. R. N. Anthony, H. P. Possingham, and P. J. Mumby. 2016. Controlling range expansion in habitat networks by adaptively targeting source populations. Conservation Biology **30**:856-866.

Hock, K., N. H. Wolff, S. A. Condie, K. R. N. Anthony, and P. J. Mumby. 2014. Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. Journal of Applied Ecology **51**:1188-1196.

Hock, K., N. H. Wolff, J. C. Ortiz, S. A. Condie, K. R. N. Anthony, P. G. Blackwell, and P. J. Mumby. 2017. Connectivity and systemic resilience of the Great Barrier Reef. Plos Biology **15**.

Hughes, T. P., K. D. Anderson, S. R. Connolly, S. F. Heron, J. T. Kerry, J. M. Lough, A. H. Baird, J. K. Baum, M. L. Berumen, T. C. Bridge, D. C. Claar, C. M. Eakin, J. P. Gilmour, N. A. J. Graham, H. Harrison, J. P. A. Hobbs, A. S. Hoey, M. Hoogenboom, R. J. Lowe, M. T. McCulloch, J. M. Pandolfi, M. Pratchett, V. Schoepf, G. Torda, and S. K. Wilson. 2018. Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science **359**:80-+.

Hughes, T. P., A. H. Baird, D. R. Bellwood, M. Card, S. R. Connolly, C. Folke, R. Grosberg, O. Hoegh-Guldberg, J. B. C. Jackson, J. Kleypas, J. M. Lough, P. Marshall, M. Nystrom, S. R. Palumbi, J. M. Pandolfi, B. Rosen, and J. Roughgarden. 2003. Climate change, human impacts, and the resilience of coral reefs. Science **301**:929-933.

Hughes, T. P., J. T. Kerry, M. Alvarez-Noriega, J. G. Alvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, T. C. Bridge, I. R. Butler, M. Byrne, N. E. Cantin, S. Comeau, S. R. Connolly, G. S. Cumming, S. J. Dalton, G. Diaz-Pulido, C. M. Eakin, W. F. Figueira, J. P. Gilmour, H. B. Harrison, S. F. Heron, A. S. Hoey, J. P. A. Hobbs, M. O. Hoogenboom, E. V. Kennedy, C. Y. Kuo, J. M. Lough, R. J. Lowe, G. Liu, M. T. M. Cculloch, H. A. Malcolm, M. J. Mcwilliam, J. M. Pandolfi, R. J. Pears, M. S. Pratchett, V. Schoepf, T. Simpson, W. J. Skirving, B. Sommer, G. Torda, D. R. Wachenfeld, B. L. Willis, and S. K. Wilson. 2017. Global warming and recurrent mass bleaching of corals. Nature **543**:373-+.

Kininmonth, S. J., G. De'ath, and H. P. Possingham. 2010. Graph theoretic topology of the Great but small Barrier Reef world. Theoretical Ecology **3**:75-88.

Leslie, L. M., D. J. Karoly, M. Leplastrier, and B. W. Buckley. 2007. Variability of tropical cyclones over the southwest Pacific Ocean using a high-resolution climate model. Meteorology and Atmospheric Physics **97**:171-180.

Logan, C. A., J. P. Dunne, C. M. Eakin, and S. D. Donner. 2014. Incorporating adaptive responses into future projections of coral bleaching. Glob Chang Biol **20**:125-139.

Lough, J. M., K. D. Anderson, and T. P. Hughes. 2018. Increasing thermal stress for tropical coral reefs: 1871-2017. Scientific Reports **8**.

MacNeil, M. A., C. Mellin, M. S. Pratchett, J. Hoey, K. R. N. Anthony, A. J. Cheal, I. Miller, H. Sweatman, Z. L. Cowan, S. Taylor, S. Moon, and C. J. Fonnesbeck. 2016. Joint estimation of crown of thorns (Acanthaster planci) densities on the Great Barrier Reef. Peerj **4**.

Marshall, P. A., and A. H. Baird. 2000. Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. Coral Reefs **19**:155-163.

Maynard, J. A., K. R. N. Anthony, P. A. Marshall, and I. Masiri. 2008. Major bleaching events can lead to increased thermal tolerance in corals. Marine Biology **155**:173-182.

Morello, E. B., E. E. Plaganyi, R. C. Babcock, H. Sweatman, R. Hillary, and A. E. Punt. 2014. Model to manage and reduce crown-of-thorns starfish outbreaks. Marine Ecology Progress Series **512**:167-183.

Plaganyi, E. E., N. Ellis, L. K. Blamey, E. B. Morello, A. Norman-Lopez, W. Robinson, M. Sporcic, and H. Sweatman. 2014. Ecosystem modelling provides clues to understanding ecological tipping points. Marine Ecology Progress Series **512**:99-113.

Puotinen, M., J. A. Maynard, R. Beeden, B. Radford, and G. J. Williams. 2016. A robust operational model for predicting where tropical cyclone waves damage coral reefs. Scientific Reports **6**.

Puotinen, M. L. 2007. Modelling the risk of cyclone wave damage to coral reefs using GIS: a case study of the Great Barrier Reef, 1969-2003. International Journal of Geographical Information Science **21**:97-120.

Sampayo, E. M., T. Ridgway, P. Bongaerts, and O. Hoegh-Guldberg. 2008. Bleaching susceptibility and mortality of corals are determined by fine-scale differences in symbiont type. Proceedings of the National Academy of Sciences of the United States of America **105**:10444-10449.

van Woesik, R., K. Sakai, A. Ganase, and Y. Loya. 2011. Revisiting the winners and the losers a decade after coral bleaching. Marine Ecology Progress Series **434**:67-76.

Walsh, K. J. E., K. C. Nguyen, and J. L. McGregor. 2004. Fine-resolution regional climate model simulations of the impact of climate change on tropical cyclones near Australia. Climate Dynamics **22**:47-56.

Wenger, A. S., D. H. Williamson, E. T. da Silva, D. M. Ceccarelli, N. K. Browne, C. Petus, and M. J. Devlin. 2016. Effects of reduced water quality on coral reefs in and out of no-take marine reserves. Conservation Biology **30**:142-153.

Wolfe, K., A. Graba-Landry, S. A. Dworjanyn, and M. Byrne. 2015. Larval Starvation to Satiation: Influence of Nutrient Regime on the Success of Acanthaster planci. Plos One **10**.

Wolff, N. H., E. T. da Silva, M. Devlin, K. R. N. Anthony, S. Lewis, H. Tonin, R. Brinkman, and P. J. Mumby. 2018. Contribution of individual rivers to Great Barrier Reef nitrogen exposure with implications for management prioritization. Marine Pollution Bulletin **133**:30-43.

Wolff, N. H., A. Wong, R. Vitolo, K. Stolberg, K. R. N. Anthony, and P. J. Mumby. 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs **35**:613-623.

Wooldridge, S., J. Brodie, and M. Furnas. 2006. Exposure of inner-shelf reefs to nutrient enriched runoff entering the Great Barrier Reef Lagoon: Post-European changes and the design of water quality targets. Marine Pollution Bulletin **52**:1467-1479.

APPENDIX B2 – DETAILED DESCRIPTION OF REEFMOD-GBR AND SIMULATION RESULTS

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B2.1 General description

ReefMod is a spatially explicit model of coral population dynamics initially developed for Caribbean coral reefs (Mumby et al. 2007). The model has been continuously improved (Mumby et al. 2014, Bozec et al. 2015, 2016) and was recently adapted to simulate coral dynamics on a typical Pacific reef (Ortiz et al. 2014). The model is individual-based and simulates the settlement, growth and mortality of coral colonies with a six-month time step on a two-dimensional grid lattice of 20 × 20 cells each of which approximates 1m^2 of the reef floor (Fig. 27). Each grid cell can be occupied by multiple coral colonies of different functional groups and by a mixture of reef algae. The grid is toroidal (i.e. wrapped around) so that every cell has the same number of neighboring cells. While the spatial dynamics captured on a grid lattice are scale-invariant (i.e. larger domains give the same demographic outputs under the same environmental forcing), the variability of coral colonisation on a reef is reproduced through a stochastic initialisation of corals (randomised initial cover, size structure and placement on the grid) and the simulation of 40 replicate model runs for each parameter scenario.

Corals are modelled by their size and belong to six functional groups:

- Plating corals (e.g. *Acropora hyacinthus*, *Acropora cytherea*)
- Arborescent (staghorn) corals (e.g. *Acropora muricata*, *Acropora nobilis*, *Acropora robusta*)
- Corymbose/small branching acroporids (e.g. *Acropora millepora*, *Acropora humilis*)
- Pocilloporids and other non-acroporid corymbose (e.g. *Stylophora pistillata*)
- Small massive/submassive/encrusting corals (e.g. *Lobophylliidae*, favids, *Goniastrea*)
- Large massive (*Porites lutea*, *Porites lobata*, *Porites australiensis*).

A focus on Acropora corals is justified as they represent the key habitat-forming species on the Reef and account for around 70 percent of the coral biodiversity in the Indo-Pacific region (Wallace 1999). Other model agents include patches of long turf, encrusting fleshy (i.e. *Lobophora*) and upright fleshy macroalgae. Ecological interactions and coral demographics are explicit and occur at colony scales following probabilistic rules. Spatially explicit grazing maintains macroalgae in a cropped state, which facilitates coral settlement and growth. Acute disturbances such as bleaching, or cyclones can occur randomly or following specified scenarios. Their impact on corals is group-specific based on empirical observations.

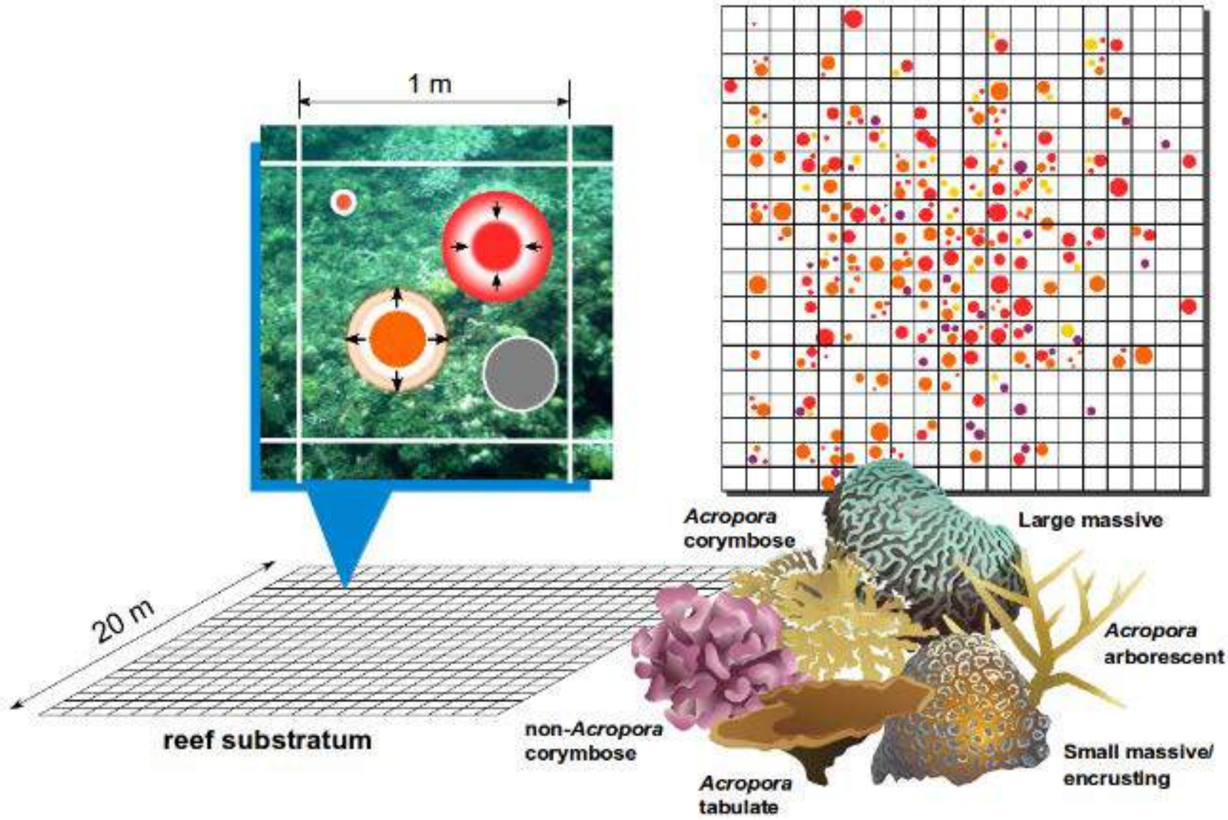


Figure 27: Schematic representation of the reef ecosystem model (ReefMod). Individual coral colonies are typified by circular areas of variable size. Corals settle, grow, shrink and die in a virtual 20m×20m environment as they do in situ. Demographic rates are specific to the six modelled coral groups. Graphics: IAN image library and YM Bozec.

For simulating coral dynamics on the Great Barrier Reef, ReefMod was further developed to integrate population dynamics of the coral-feeding crown-of-thorns starfish (*Acanthaster* spp). In addition, coral demographics were refined with explicit mechanisms driving the early-life stages of corals: coral reproduction, coral settlement, and growth and mortality of coral recruits and juveniles. A new parameterisation of coral recruitment, growth and mortality (including bleaching mortality) was developed based on recent empirical data from the Reef. For RRAP, we implemented natural processes of rubble formation and stabilisation which affect coral juvenile demographics. The model was also augmented with recent modelling of algal succession dynamics and grazing (Bozec et al. 2019); however, due to limited data on fish abundance and body size, we assumed full grazing efficiency across the entire Reef, so that reef algae were maintained in a cropped state everywhere. The process of grazing will be revisited in the RRAP R&D Program by modelling functional fish grazing for different levels of fishing and habitat complexity (Mumby 2006, Bozec et al 2013, 2016) and by accounting for spatial and temporal variations in algal productivity as informed by the eReefs biogeochemical model (Chen et al. 2011, Herzfeld et al. 2016). These new implementations lead to a comprehensive representation of key reef processes and interactions (Fig 28).

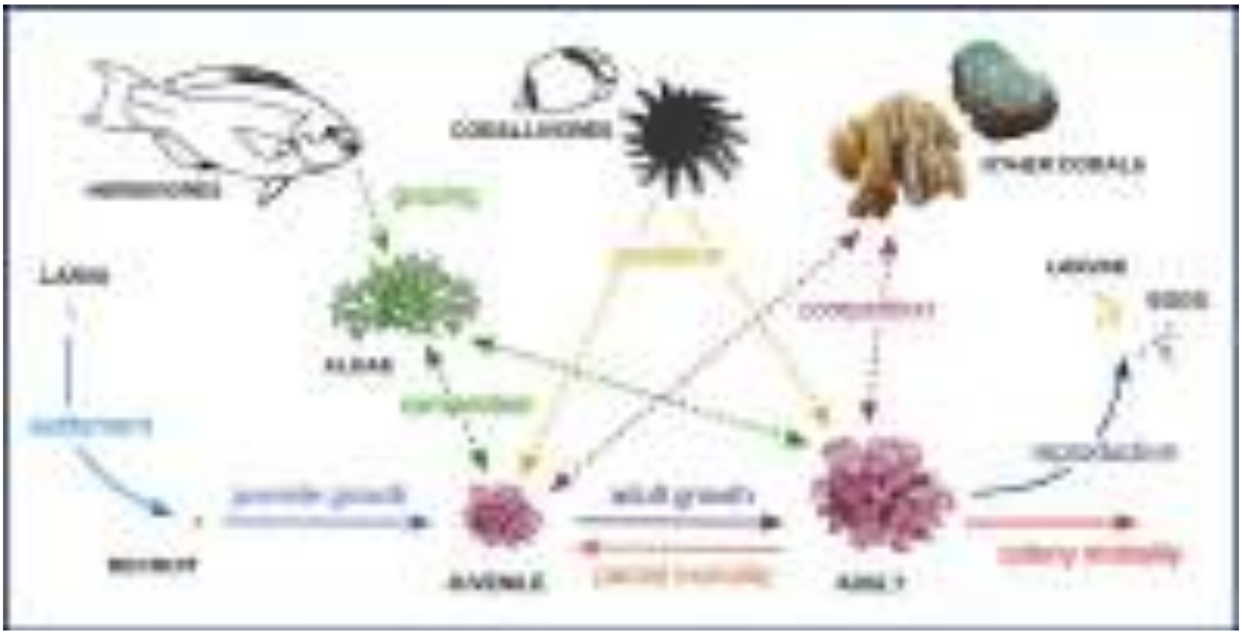


Figure 28: Demographic processes (solid arrows) and ecological interactions (dashed arrows) affecting corals in the reef ecosystem model (ReefMod). Processes are spatially explicit across a 20m×20m reef surface and occur at the level of coral individual. Graphics: IAN image library and YM Bozec.

To model spatially realistic reef dynamics across the entire Reef, the model was extended to integrate multiple coral populations within their spatial context of disturbances. Each reef of the Great Barrier Reef marine park (3,806 reef polygons) is represented by a 20m × 20m grid lattice to simulate coral demographics in response to coral's fluctuating environment (temperature, water quality) and exposure to acute stress (cyclones, extreme heatwaves, river runoffs, crown-of-thorns starfish outbreaks). Reef populations are connected through connectivity matrices of larval dispersal of coral and crown-of-thorns starfish (Hock et al. 2014, 2017) and subject to water quality forcing as predicted in space and time by the eReefs modelling platform (Chen et al. 2011, Herzfeld et al. 2016). The model is spatially explicit in three ways: first by simulating the demographic processes of individual coral colonies and crown-of-thorns starfish populations on a reef landscape, second by linking coral and crown-of-thorns starfish demographics to their ambient environment (water quality on a given reef and exposure to cyclones and thermal stress), and third by connecting reefs in a network that represents inter-reef larval exchanges for both crown-of-thorns starfish and corals.

B2.1.1 Coral metapopulation dynamics

Larval connectivity

Dispersal of coral and crown-of-thorns starfish larvae was simulated to determine the connectivity relationships among 3806 individual reefs in the region (Hock et al. 2017). Briefly, larval dispersal was initialised by releasing the particles at the assumed dates of mass coral spawning across the Reef. Dispersal of larvae released in the water column was simulated with the Connie particle tracking tool (Condie et al. 2012), www.csiro.au/connie2/) which uses the same hydrodynamic model as eReefs to generate a three-dimensional model of particle dispersal driven by ocean circulation. This model has hourly time steps and a spatial resolution of hydrodynamic forces over a 4km grid. Larvae that came within 1km of a reef polygon during dispersal would then contribute recruits to that reef, and these recruits were added to the population dynamics models on that reef. The strength of connection between a source and a sink was determined by the number of larvae that reached another reef. This was further modified to represent time-sensitive survival and development characteristics of the modelled species (Connolly and Baird 2010, Pratchett et al. 2014, Hock et al. 2017), with the probability that a particle would successfully contribute to larval supply at a sink reef dependent on time between spawning and arrival at the sink reef. The simulation of larval dispersal was repeated for designated spawning times over the six years for which the hydrodynamic models were available: summers of 2010-11, 2011-12, 2012-13, 2014-15, 2015-16, and 2016-17 (see below).

Larval supply and recruitment

On a given reef, corals produce offspring following an allometric relationship between colony size and fecundity (Hall and Hughes 1996). The number of larvae is extrapolated to the reef area before dispersion. Retention and larval transport allow estimating of a pool of incoming larvae (L) per unit of reef area, per reef, which represents the amount of coral larvae available for settlement on that reef. With a six-month time step, the model cannot capture the detailed dynamics of larval settlement and post-settlement processes that operate during the early phases of coral ontogeny. Here, these processes are implicitly combined to result in the establishment of six-month-old recruits, which is the assumed age of corals that successfully passed through the suite of demographic bottlenecks (Doropoulos et al. 2016) and survived at the end of the summer step (broadcast spawning occurs at the beginning of summer). Assuming recruitment is density-dependent (e.g. due to compensatory mechanisms affecting the survival of larvae in the water column and settlers on the reef), the number of six-month-old recruits ($N_{recruits}$) is a sigmoid function of the available pool of larvae L:

$$N_{recruits} = \frac{\alpha \cdot L}{\beta + L}$$

where α is the maximum density of recruit (asymptote) able to settle and survive in the following six months and β is the stock of larvae required to produce half the maximum settlement. Consecutively, a number of recruits is generated in each 1m^2 grid cell from a Poisson distribution with settlement event rate λ calculated as:

$$\lambda = N_{recruits} \times A$$

where A is the proportional space available for settlement in a cell (i.e. uncolonised space). This assumes that the probability of recruitment is directly proportional to the cover of substratum that is suitable for settlement (Connell 1997).

Parameters α and β were calibrated against empirical data of juvenile density on natural substrates. With β set to 50 millions larvae per 400m^2 (i.e. the surface of a reef grid) and coral specific values of α in the range 0.5–2.5 m-2 (0.5 m-2 for arborescent Acropora, 2.5 m-2 for plating and corymbose Acropora, and 1.5 m-2 for the other 3 coral groups), the model predicts juvenile (<50mm diameter) density values in the range 4–10 m-2 consistent with recent Reef observations across a latitudinal gradient (Figure 29, Trapon et al. 2013).

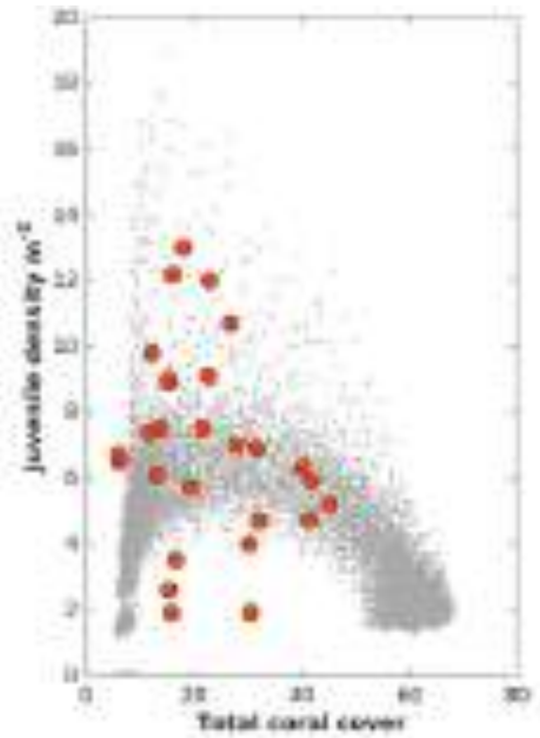


Figure 29: Number of juveniles as predicted by the model (grey dots) and as observed (red dots) by Trapon et al. (2013) over a range of coral reef states. The modelled juvenile densities were obtained by simulating coral recovery from a five percent cover in the Cairns region, thus reflecting changes in coral recruitment with the regional build-up of coral reproductive stock and the concurrent reduction of settlement space.

Post-settlement demographics

Corals enter the model as six-month-old recruits and become juveniles at the next step if allowed to grow (i.e. coral recruitment is processed after all other coral demographic processes, but before disturbances). The growth rate of juveniles is the same for all coral species and fixed to 0.5cm radial extension every six months (Doropoulos et al. 2015, 2016) until they reach a size threshold of 10cm^2 (~3.5cm in diameter), after which they acquire their adult growth rate (Fig. 30A) and survival significantly improves. For example, three-year-old corals of the corymbose/small branching acroporids group would have a diameter of 12.4cm in the absence of partial mortality (Fig. 30B), which falls within the range of observed diameters (7.8–13.7cm) for Acropora millepora at this age by (Baria et al. 2012) in the Philippines.

At this size threshold of 10cm^2, the minimum age is ~two-years-old (i.e. if no partial mortality event has occurred yet) and corals have escaped the most severe post-settlement bottlenecks (Vermeij and Sandin 2008, Doropoulos et al. 2016). Mortality until the 10cm^2 size threshold was fixed to 0.1 per six months which corresponds to the average mortality recorded for 1cm diameter classes in the range 1–4cm on a reef slope at Heron Island (Doropoulos et al. 2015).

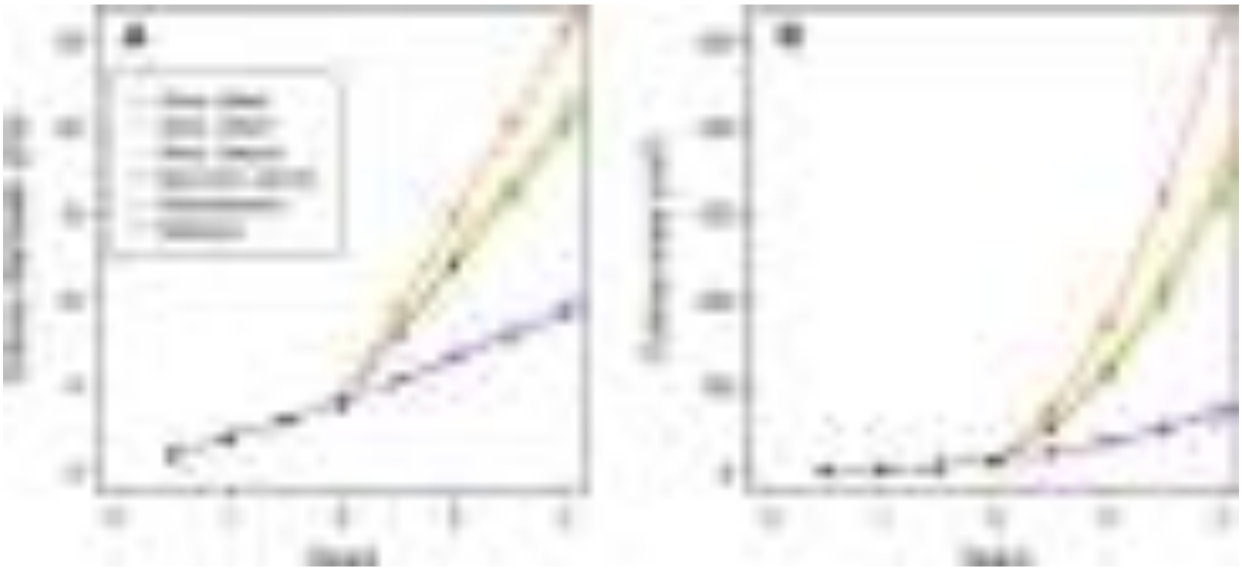


Figure 30: Post-settlement growth of the six modelled coral groups showing theoretical change in colony diameter (A) and colony area (B) within four years post-settlement. Corals are modelled from the stage of recruit (six-months-old) and growth by 0.5cm radial increment every six months until they reach a size threshold of $10cm^2$ (~3.5cm in diameter, ~two-year-old recruits) where they acquire their adult growth rate. This size threshold is also use for switching mortality rate from 0.1 to 0.02 per six months.

B2.1.2 Water quality

Nutrients, sediments and other pollutants run off from river catchments and episodically expose coral reefs to varying loads over varying spatial extents and timeframes (e.g. following extreme rainfall and river flood events). To capture these dynamics, exposure to run-off was assessed using the eReefs modelling platform developed by CSIRO. The eReefs coupled physical biogeochemical model considers a range of physical (meteorological, river and wave forcing), sediment (sinking, re-suspension etc.) and biogeochemical (plankton dynamics, benthic productivity, re-mineralisation, de-nitrification etc.) processes to simulate water quality (Robson et al. 2013, Herzfeld et al. 2016, Baird et al. 2017). To model the effects of changing water quality in time and space on coral and crown-of-thorns starfish dynamics, we used the retrospective daily predictions of suspended sediments and chlorophyll at 4km × 4km resolution with the best available forcing provided by model configurations GBR4_H2p0_B2p0_Chyd_Dcrt (12/2010–10/2016) and GBR4_H2p0_B2p0_Chyd_Dnrt (11/2016–12/2017). Suspended sediment concentrations (SSC) were obtained by summing together the spatial layers of Mud, CarbSand (carbonate sand) and FineSed (fine sediment) representing small-sized re-suspending particles of different optical properties and origin. While Mud and CarbSand describe re-suspending particles from the deposited sediments, FineSed tracks the particles entering the Reef through river catchments.

Impacts of suspended sediments on coral demographics

For modelling coral demographics, we focus on suspended sediment concentrations (SSC) predicted at different depths over different seasons. Suspended sediment influences many aspects of coral biology (Anthony et al. 2009, Jones et al. 2015) but are only considered here at the early life-history stages of broadcast spawner corals: (i) fertilisation followed by embryo development before transportation of coral larvae off the reef (hereafter referred to as “reproduction success”), (ii) survival of corals recruits within six months following settlement, and (iii) growth of coral juveniles. Spatio-temporal predictions of coral reproduction and recruitment success were obtained by combining maps of suspended sediments with dose-response curves derived from recent experimental Great Barrier Reef data (Humanes et al. 2017b, 2017a).

Using *Acropora tenuis* as a model species, Humanes et al. (2017b) assessed in tank experiments the effects of SSC, temperature and nutrient concentrations on fertilisation success, embryo development, larval development and settlement success. In a first experiment, they demonstrated an effect of increasing SSC (0, 5, 10, 30 and 100 mg.L-1) on the proportion of fertilised eggs (~1.5 hours after fertilisation) while nutrient concentrations and temperature had no or little impact. A dose-response curve of fertilisation success to SSC can be obtained by fitting a simple linear model to the proportion of fertilised eggs across all SSC and nutrient treatments at ambient temperature (Fig. 31A). In a second experiment, Humanes et al. (2017b) exposed embryos (eight-hour-old) to increasing SSC, nutrients and temperature, until they became ciliated larvae (~36-hour-old). Coral larvae were then maintained in controlled conditions without any stressor and the proportion of settled larvae was recorded after 24 hours of induced settlement. While early (embryo) stress exposure did not affect survival to the settlement stage, larval settlement success responded significantly to all stressors, with SSC having the strongest effect. Here, SSC treatments were combined with the low and medium nutrient treatment at ambient temperature to fit a dose-response curve of relative settlement success (Fig. 31B). No significant effects of SSC were observed after exposure at later development stages. Finally, the two response curves were combined into a single one that predicts the relative success of coral reproduction as a composite function of fertilisation success and future capacity (i.e. competency) to settle (Fig. 31C). This function can be used to estimate the number of competent larvae produced on a reef exposed to SSC during spawning events (i.e., prior to dispersion).

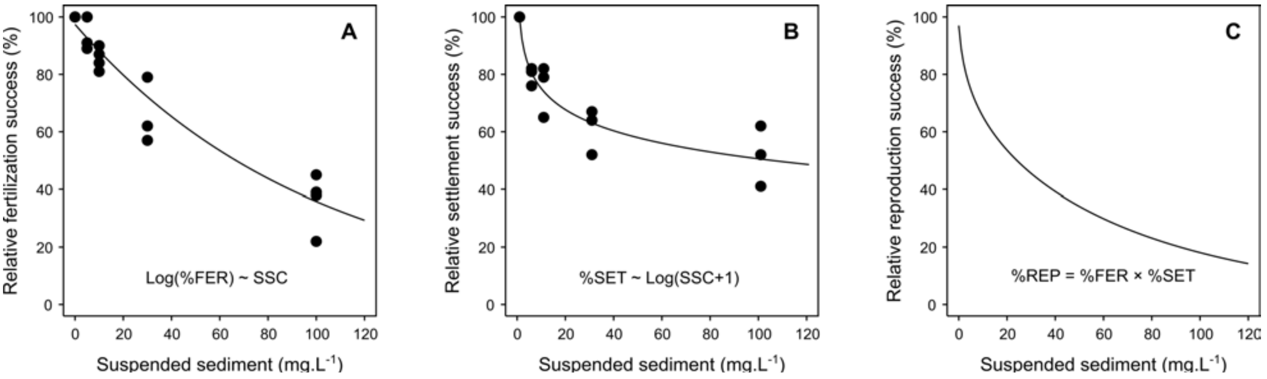


Figure 31: Modelling of dose-response relationships of coral pre-settlement processes to concentrations of suspended sediment (SSC) from experimental observations (Humanes et al. 2017b). (A) Experimental data (dots) of relative fertilisation success (percent fertilised eggs relative to control) fitted with a linear model (R2=0.88, n=20). (B) Experimental data (dots) of relative settlement success (percent settled larvae relative to control) following exposure of embryos to increasing SSC, fitted with a linear model (R2=0.88, n=15). (C) Empirical response curve of percent 'reproduction success' as the combined success of gamete fertilisation and development of competent larvae relative to reef waters devoid of suspended sediments (i.e. on reefs where SSC = 0 mg.L-1).

Spawning corals release combined egg-sperm bundles that immediately ascend to the surface (Richmond 1997, Jones et al. 2015). Gamete bundles then break apart within an hour and fertilisation takes place near to the surface, with first cleavage generally occurring within six hours. To capture sediment exposure at these early (<36-hr) development stages of broadcast coral larvae, daily spatial predictions of near-surface (-0.5m) SSC were extracted from eReefs at the assumed dates of mass coral spawning across the Reef. Spawning dates between 2011 and 2016 (C. Doropoulos, CSIRO, pers. comm.) account for consecutive (split) spawning events and patterns of synchrony across the northern, central and southern regions. From the assumed spawning date in a given region, the 4km × 4 km pixeled SSC values were averaged over three consecutive days to account for spatio-temporal variations in spawning synchrony and embryo development. The resulting mean SSC values were further averaged over multiple spawning events (Fig. 32A). Predictions of coral reproduction success were calculated for each pixeled SSC and assigned to the nearest reef polygon, thus enabling the mapping of reproduction success at a reef-by-reef scale (Fig. 32B).

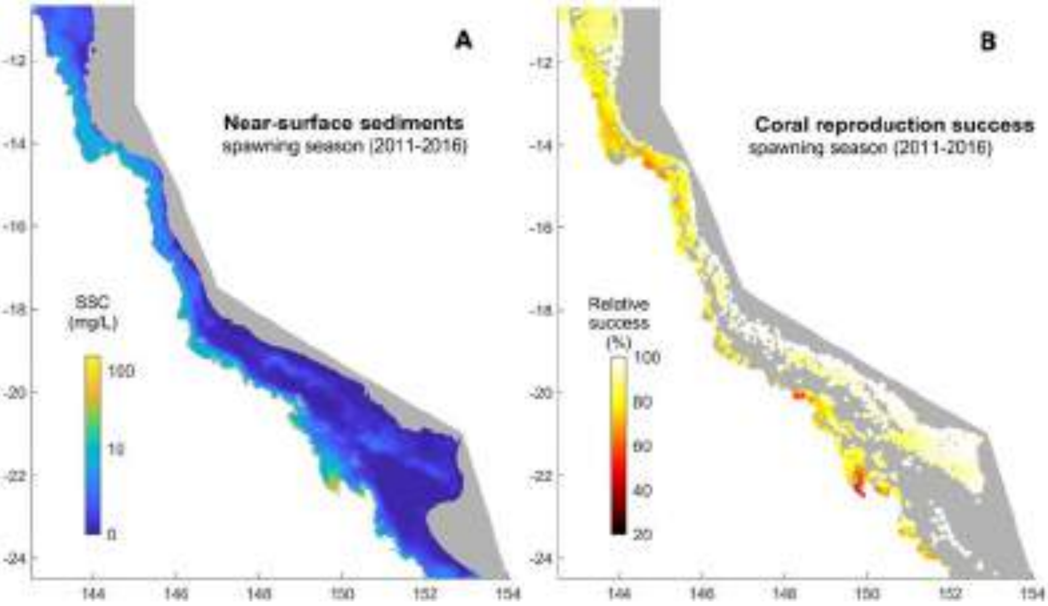


Figure 32: Great Barrier Reef 2011–2016 mean predictions of (A) near-surface suspended sediment concentrations (SSC) at 4km ×4km resolution during mass coral spawning (note the logarithmic scale) and (B) relative success of coral reproduction at 3806 reef centroids (dots) inferred from SSC using the empirical relationship shown on Fig. 31C.

Suspended sediments also affect the early-life history of corals after dispersion and settlement. In another series of experiment Humanes et al. (2017a) assessed the impacts of increasing SSC on the growth and survival of three- to six-month-old recruits of three corymbose/small branching corals: Acropora tenuis, Acropora millepora and Pocillopora acuta. After 40 days of exposure to crossed treatments of nutrients and SSC, a significant effect of SSC was detected on the survival of A. millepora recruits, but not on the other two species; nutrient concentrations had no significant effect on any species. Here, SSC treatments at low and high nutrient concentrations were combined to fit a dose-response curve of the survival of Acropora recruits relative to baseline (null SCC) treatments (Fig. 33A). For the sake of simplicity, we assumed that one dose-response curve can fit all species (Fig. 33B).

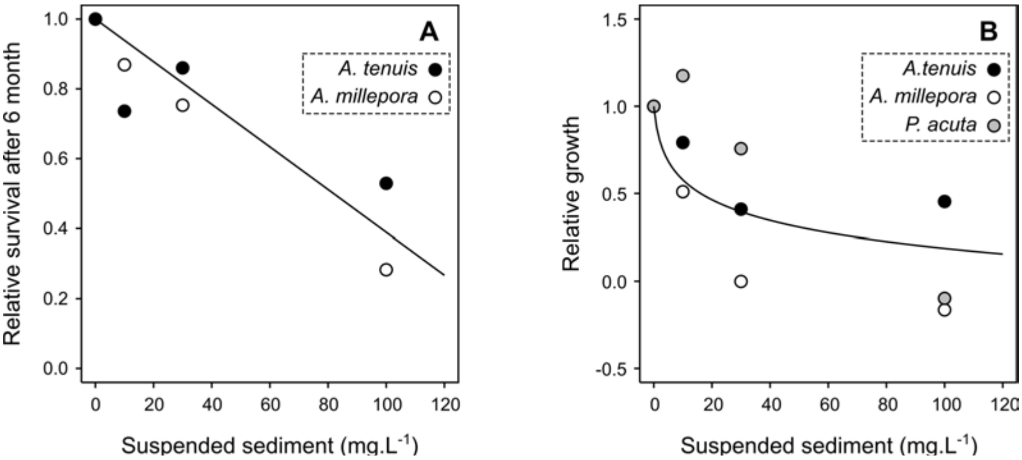
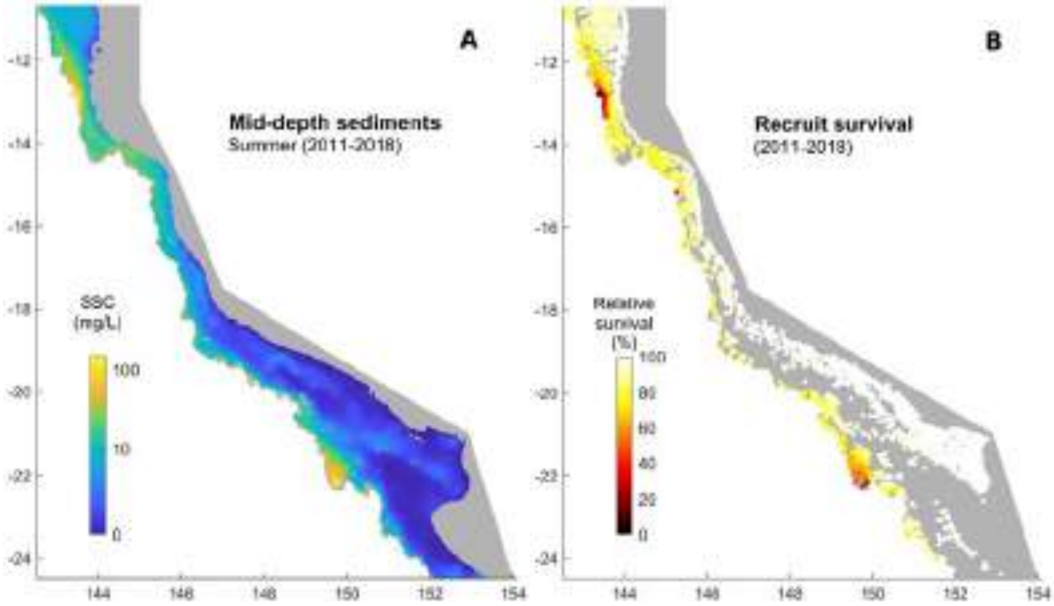


Figure 33: Modelling of dose-response relationships of post-settlement survival and growth following exposure to suspended sediment concentrations for 40 days based on the experimental data (dots) of (Humanes et al. 2017a). (A) Relative survival (survived fraction relative to control, here extrapolated to 6 months) of three- to six-month-old coral recruits following sustained exposure to SSC fitted with a linear model (R2=0.89, n=8). (B) Proportional growth of coral recruits relative to control following exposure of embryos to increasing SSC (log-transformed), fitted with a linear model (R2=0.79, n=12).

Exposure of *Acropora* recruits (i.e. 1cm^2 corals) to suspended sediment across the Reef was captured from eReefs daily predictions of SSC (4km × 4 km pixel) at mid-depth (~ -6m) during the 2011-2018 summer months (November to April, Fig. 34A). An estimate of recruit survival was produced for each daily value of pixeled SSC from the empirical dose-response described above (after downscaling to daily survival). Predicted daily survivals were combined over each summer period and assigned to the nearest reef polygon. This resulted in six spatial layers (one for each recruitment season between 2011 and 2016) of six-month cumulative survival of *Acropora* recruits at a reef-by-reef scale (Fig. 34B).

Similarly, spatial layers predicting the growth potential of coral juveniles (i.e. below 2.5cm diameter) were derived by averaging the pixeled SSC values in summer (six months from November to April) and winter (six months from May to October) for every year of the 2011-2016 period (Fig. 34C). Pixeled predictions of relative juvenile growth (all coral species) were assigned to the nearest reef polygon (Fig. 34D).



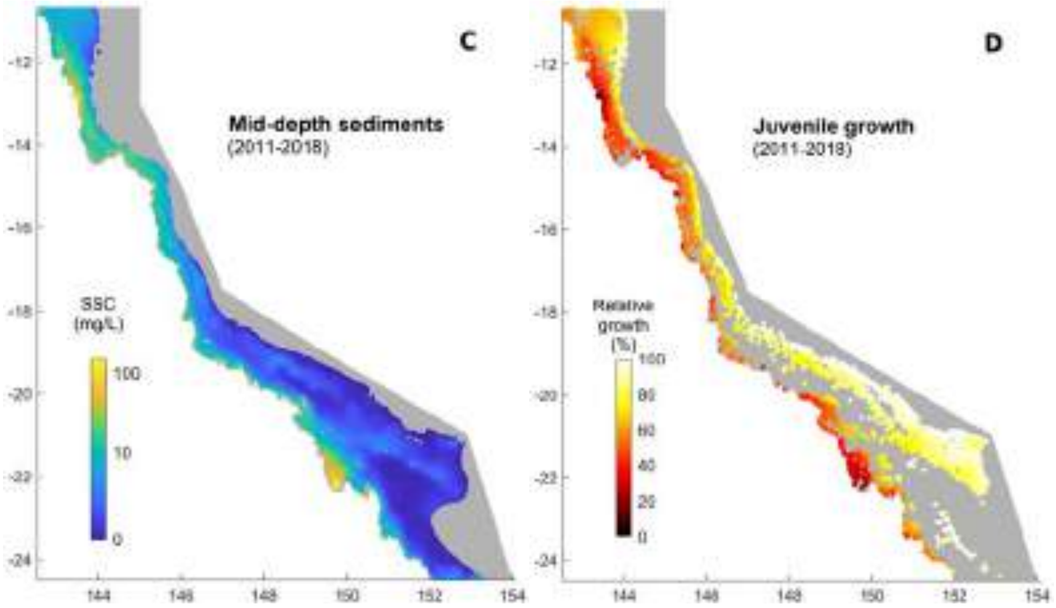


Figure 34: Great Barrier Reef 2011–2018 mean predictions of suspended sediment concentrations (SSC) and impacts on coral post-settlement demographics. (A) Mid-depth (~ -6m) SSC during summer months averaged from November to April over the 2011–2018 period (note the logarithmic scale) and (B) corresponding reef-by-reef predictions (dots) of relative survival of Acropora recruits within six months of settlement (survival of other corals assumed to be insensitive to SSC). (C) Mid-depth (~ -6m) SSC averaged over each season and year (note the logarithmic scale) and (D) corresponding reef-by-reef predictions of relative growth of coral juveniles (all coral species).

Impacts of chlorophyll concentrations on crown-of-thorns starfish demographics

Concentrations of total chlorophyll a (Chla) at 4km × 4km resolution were extracted from eReefs between 2011 and 2016 during the spawning season of crown-of-thorns starfish. Daily maximum Chla concentrations from December to January were used as predictors of the relative survival of crown-of-thorns starfish larvae before dispersal following Fabricius et al. (2010).

B2.1.3 Crown-of-thorns starfish outbreaks dynamics

Outbreak dynamics of the crown-of-thorns starfish (Acanthaster planci, crown-of-thorns starfish) are simulated using a simple cohort model (Fig. 35). The model is structured by age (six-month age classes) and integrates age-specific rates of mortality (Fig. 36) fecundity and coral consumption (e.g. Kettle and Lucas 1987, Keesing and Lucas 1992). crown-of-thorns starfish release their gametes in summer (December-January) and the resulting number of larvae is affected by the ambient concentration of chlorophyll a (Chl-a) as predicted by eReefs. High chlorophyll concentrations promote the survival of crown-of-thorns starfish larvae (Fabricius et al. 2010) and connectivity information (Hock et al. 2014) determines the amount of crown-of-thorns starfish larvae that are retained or distributed to other reefs. The stock of crown-of-thorns starfish larvae that is available for settlement on a given reef is thus a function of local retention and external supply. The amount of corals consumed varies between coral species, and when coral cover drops below five percent the population of coral-feeding crown-of-thorns starfish dies due to starvation.

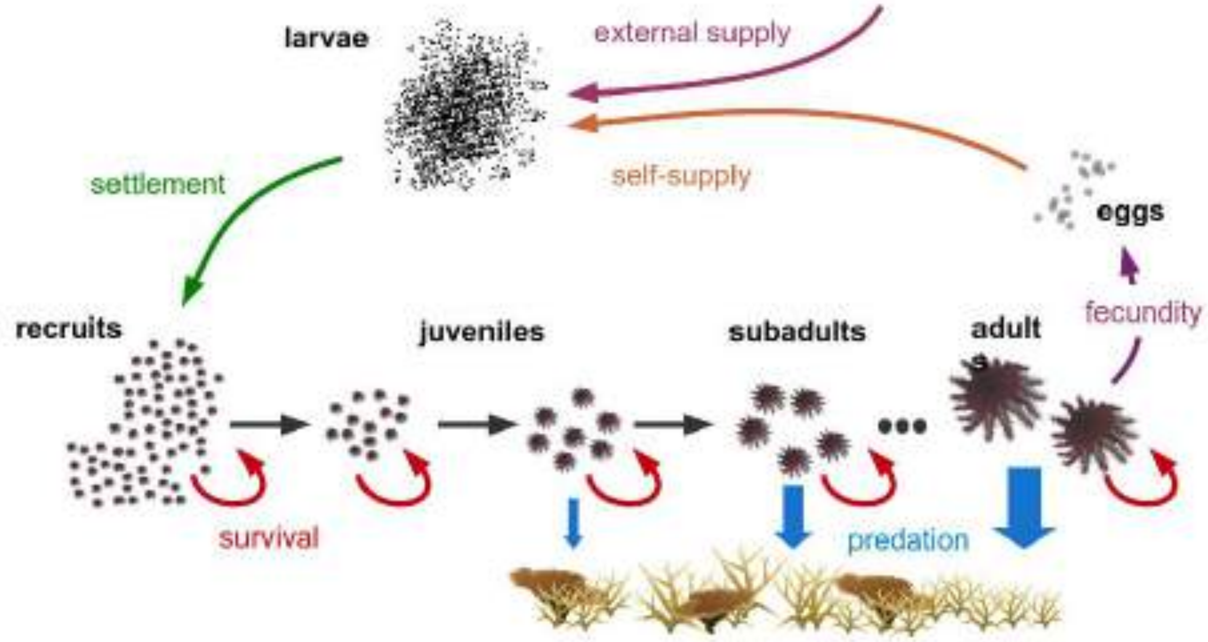


Figure 35: Modelling of crown-of-thorns starfish population dynamics and impact on corals with the demographic processes parameterised using empirical data. The model describes the fate of crown-of-thorns starfish cohorts recruiting in summer and subject to size-specific survival during their life. Settlement occurs from a pool of larvae that results from the retention of locally produced offsprings and the incoming of larvae from connected reef populations. Individuals in one year+ cohorts feed on corals at size-specific consumption rates.

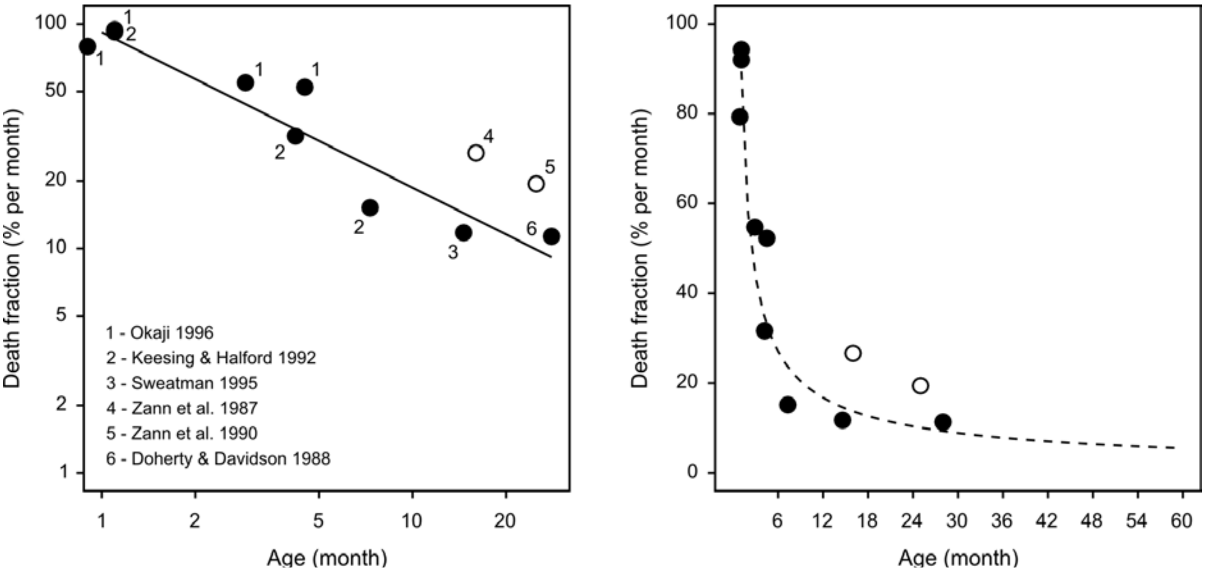


Figure 36: Point estimates of crown-of-thorns starfish mortality (monthly death fraction) as a function of age (right) and log-log relationship (left). Mortality estimates are based on survival rates scaled to one month. Age represents the median age of the cohort during the study period. Empty circles denote estimates excluded from the model due to the prevalence of disease (Zann et al. 1987) and low accuracy in abundance estimates (Zann et al. 1990). Model statistics: n = 8, intercept significantly non null at p<10-7, slope significantly non null at p<10-4, adjusted R2 = 0.89.

B2.1.4 Cyclones

Whole-colony and partial mortality of adult coral colonies is a function of colony size and storm strength (Edwards et al., 2011, Bozec et al. 2015), with group-specific adjustments to account for the sensitivity of the different growth forms: ×10 for arborescent Acropora, ×8 for plating and corymbose/small-branching corals, ×1 for massive and encrusting forms. Scouring by sand during a cyclone causes 80 percent whole-colony mortality in recruit and juvenile corals (Mumby, 1999).

B2.1.5 Widespread coral bleaching

Widespread coral bleaching on the Reef is assumed to be primarily driven by thermal stress (Berkelmans 2002, Hughes et al. 2017, 2018). Bleaching only occurs during summer steps following exposure maps to thermal stress based on past records (detailed in section "hindcast"), or forward projections of sea surface temperature (sea surface temperature) anomalies predicted under different warming scenarios by global climate models (detailed in section "forecast"). Coral mortality following bleaching events is a function of thermal stress (degree heating weeks) parameterised with bleaching mortalities reported during the 2016 bleaching event recorded across the Reef by Hughes et al. (2018). While this study provides one of the most comprehensive records of bleaching mortalities on corals from the Great Barrier Reef, there are few limitations: (1) Hughes et al. (2018) only recorded coral mortality at the peak of the bleaching event (over two to three weeks in March 2016), i.e. initial mortality, likely to underestimate coral mortality experienced over the entire bleaching event; (2) that the survey of bleaching mortality was performed at 2m depth, likely to overestimate any extrapolation to deeper corals; (3) that no information is available on partial mortality (i.e. only whole-colony mortality was recorded at the peak of the bleaching event), likely underestimating coral damages during the 2016 bleaching event. While a number of assumptions are required to parameterise realistic bleaching-induced mortalities, including per capita mortality rates, rates of incidence of partial mortality and extent of tissue lost due to bleaching, the observations of coral cover loss of Hughes et al. (2018) six months after the bleaching event can be used for calibration.

B2.1.6 Whole-colony mortality

An empirical relationship between coral mortality and thermal stress (degree heating weeks) was derived by regressing Hughes et al. (2018)'s observations of initial coral mortality (whole-colony mortality) against their satellite-derived 5km resolution degree heating weeks values. This simple linear model allows generating deterministic (Fig.37) or stochastic predictions (i.e. falling within the confidence intervals of predictions) of bleaching mortality for any degree heating weeks value. In the model, bleaching mortalities are generated only when thermal stress is equal or above 4°C-weeks to avoid excessive bleaching mortality at low thermal stress.

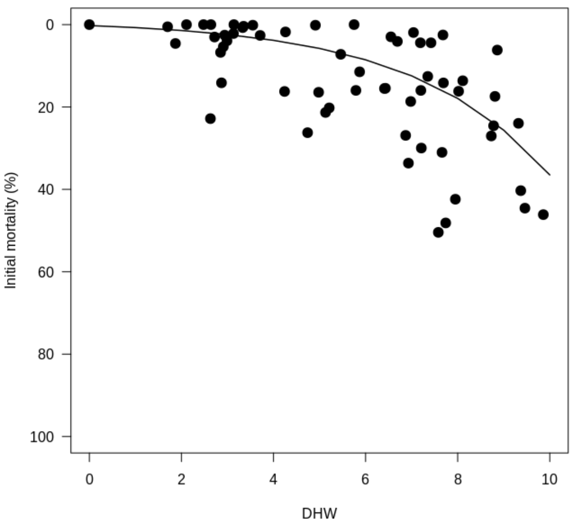


Figure 37: Initial coral mortality (dots) recorded at the peak of the 2016 bleaching events by Hughes et al. (2018) in the northern Great Barrier Reef, fitted with a linear model (modelled variable is log(mortality+1), R2=0.45).

B2.1.7 Extent of partial mortality due to bleaching

Baird and Marshall (2002) found almost no partial mortality on A. hyacinthus and A. millepora during the 1998 bleaching event on the central region of the Reef (Palm Islands Group). Consequently, the extent of partial mortality was considered minimal and fixed to five percent of colony area for the three Acropora groups (i.e. plating corals, arborescent corals and corymbose/small branching acroporids) as well as for the pocilloporid/other non-acroporid corymbose group. For small massive/submassive and large massive coral groups, this value was set respectively to 40 percent and 20 percent of colony area based on their observations on Platygyra daedalea and Porites lobota.

B2.1.8 Species-specific sensitivity to bleaching

Mortality of each coral group was further adjusted using the information on initial mortality per taxa reported by Hughes et al. (2018). Taking as a baseline an average mortality of ~20 percent across taxa, relative mortalities were estimated for each group as follows: (1) plating corals: 1.6; (2) arborescent (staghorn) corals: 1.5; (3) corymbose/small branching acroporids: 1.4; (4) pocilloporids and other non-acroporid corymbose: 1.7; (5) small massive/submassive/encrusting corals: 0.25; (6) large massive corals: 0.25.

B2.1.9 Incidence of partial mortality due to bleaching

While the study of Hughes et al. (2018) does not provide specific information about bleaching-induced partial mortality, different incidence values (i.e. the probability that a given coral exhibits partial mortality) were tested in an attempt at matching the observed losses of coral cover reported by Hughes et al. (2018). For a given thermal stress (degree heating weeks), the incidence of partial mortality is obtained by multiplying the predicted whole-colony mortality by a constant C, assuming the incidence of partial and whole-colony mortalities are correlated.

Calibration

With a value of C = 5 (i.e. the incidence of partial mortality is five times the incidence of whole-colony mortality), model simulations were able to reproduce the range of coral cover loss reported by Hughes et al. (2018) after the 2016 bleaching event (Fig. 38). This calibration was performed by simulating the impact of the 2016 bleaching for hypothetical reefs initialised with coral cover values reported by Hughes et al. (2018) before bleaching. Coral cover was dis-aggregated among the six functional groups with a community composition assumed to be representative of an outer reef of the region (following AIMS Long-term Monitoring Program for the Cairns region). Thermal stress was stimulated by randomly exposing reefs to the recorded 2016 degree heating weeks values.

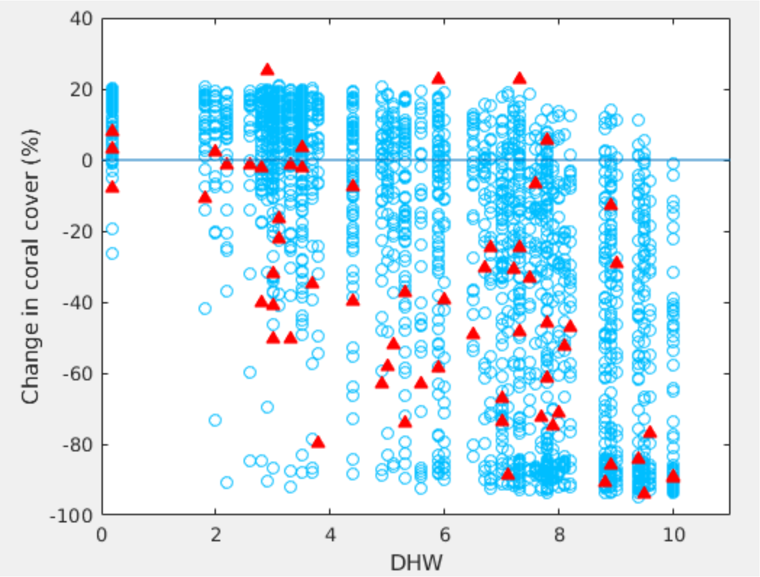


Figure 38: Stochastic predictions of coral mortality (empty blue dots) based on the degree heating weeks values observed during the 2016 bleaching, with the observations (red triangles) of Hughes et al. (2018).

B2.1.10 Rubble

Extensive coral mortality following acute disturbances (cyclones, bleaching and crown-of-thorns starfish outbreaks) generate loose coral debris that cover the reef substratum and inhibit coral recruitment (Dollar and Tribble 1993, Fox et al. 2003, Biggs 2013). The percent coral cover lost is transformed into percent rubble cover with a conversion factor of 1.5 (e.g. a loss of 20 percent coral cover produces 30 percent rubble cover) in order to account for the greater surface covered by collapsed skeletons relative to their living counterparts. Coral rubble is generated immediately after cyclones, but only three years after bleaching and crown-of-thorns starfish predation (Sano et al. 1987) to delay the structural collapse of dead skeletons relative to erosion. Assuming coral recruits do not survive on loose rubble (Fox et al. 2003, Viehman et al. 2018), the rate of juvenile survival at a given time step (0.9 per six months without suspended sediments) is reduced proportionally to the area covered by rubble. For example, with 30 percent rubble cover, the survival rate of juveniles becomes 0.9 × (1 – 0.3) = 0.63 per six months.

Loose coral rubble tends to stabilise over time due to natural processes of binding and cementation (Rasser and Riegl 2002). We modelled these dynamics using a simple exponential decay function with the assumption that 50 percent of rubble is stabilised over four years. This rate is a conservative estimate of the observed dynamics of experimental rubble stabilisation in Curaçao, Netherlands Antilles (Biggs 2013). In two reef sites, Biggs (2013) followed ~20 piles of fragments of branching Acropora (Fig. 39A) over four years, recording the number of piles stabilised by turf algae in at least one survey (‘temporary’ stabilisation). Several coral recruits were detected on the stabilised piles, suggesting that coral settlement and survival is possible during the early stages of rubble consolidation in relatively calm hydrodynamic environments. In the model, rubble stabilisation can be delayed with the addition of new coral fragments following coral mortality events. The area of rubble newly stabilised becomes epilithic algal matrix (i.e. carbonate substratum suitable for coral settlement) and increases proportionally the survival of coral juveniles. For example, the stabilisation of 20 percent of rubble covering 30 percent of the reef substratum increases juvenile survival from 0.63 per six months to 0.9 × (1 – (0.3 – 0.3 × 0.1)) = 0.68 per six months.

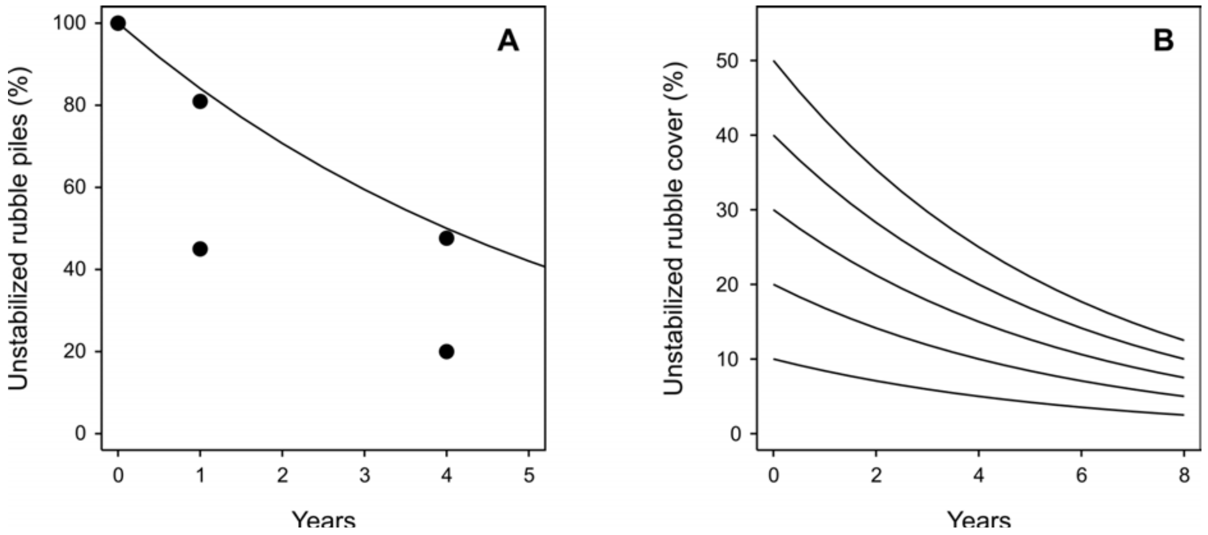


Figure 39: Modelling of rubble natural stabilisation. (A) Proportion of experimental rubble piles (dots) showing no sign of stabilisation over the course of Biggs (2013)'s in situ experiment fitted with an exponential decay function.

B2.1.11 Genetic adaptation

The model accounts for the evolutionary dynamics of coral fitness to temperature change by integrating a quantitative genetic model of thermal tolerance and adaptation. Phenotypic tolerance to increasing sea surface temperature was implemented following the polygenic model developed by Matz et al. (2018). Briefly, thermal tolerance of a coral colony is shaped by a set of quantitative trait loci that are transmitted from parents to offspring. Each thermal quantitative trait locus is associated with an effect size (in °C) and the sum of effect sizes over all loci gives the breeding value for thermal tolerance (Fig. 40). The actual phenotype is obtained by adding a normally distributed random noise to the breeding value to model imperfect heritability. This sets a specific phenotypic optimum (Topt) to every coral from which thermal fitness can be calculated relative to the ambient temperature.

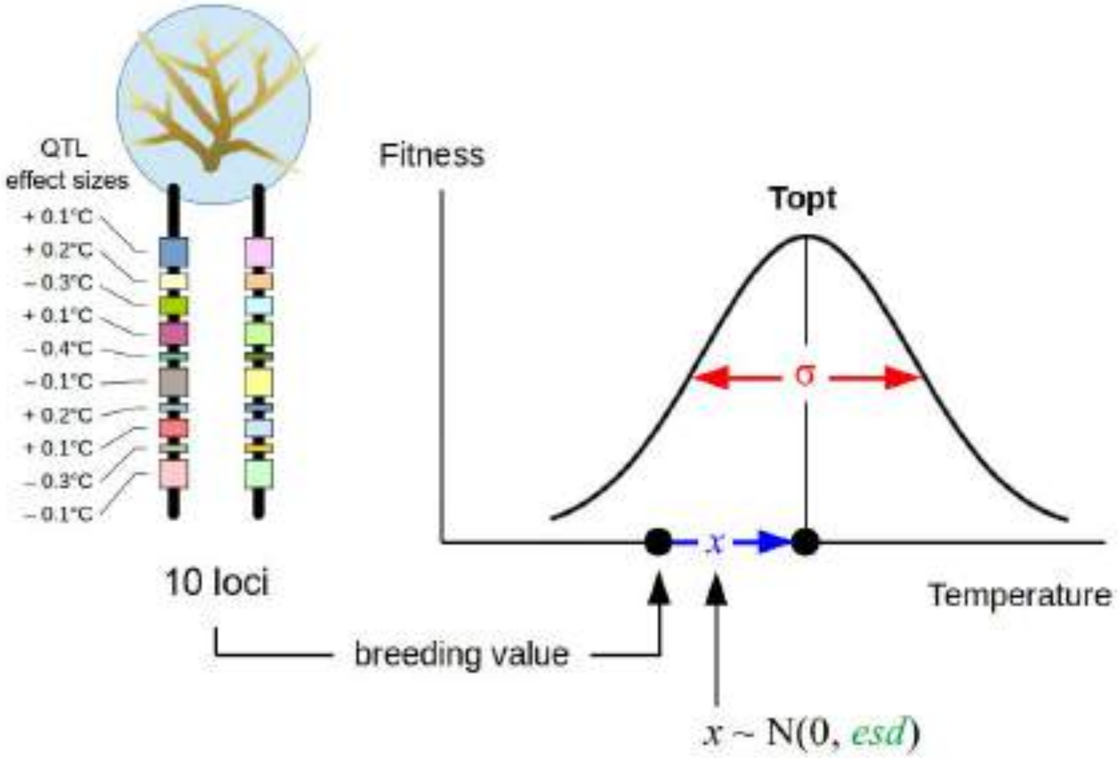


Figure 40: Modelling of thermal adaptation. Coral fitness to temperature is determined by a set of quantitative trait loci (QTL) each having a small quantitative effect (positive or negative) on thermal tolerance. For every coral individual, the sum of quantitative trait loci gives the breeding value for thermal tolerance, on which a normally distributed random noise x (blue) is added to obtain the phenotypic thermal optimum Topt. The value x represents the environmental component of the phenotypic Topt and relates to the heritability of thermal tolerance: the greater the noise the lower heritability. Thermal fitness is maximal when the ambient temperature perfectly matches the coral Topt, thus conferring a demographic advantage to the coral (growth, reproduction). Two parameters drive the efficiency of genetic adaptation: (1) the standard deviation σ (red) of the Gaussian curve that controls the slope of the fitness decline (tolerance breadth) and (2) the standard deviation esd (green) of the normally distributed random noise x.

Model burn-in: Creation of genotypes pre-adapted to warming

Model simulations start for each reef grid with an equilibrial stock of quantitative trait loci pre-adapted to warming and assumed to be representative of the genetic diversity of standing populations. This stock is generated behind-the-scene by running a model of coral generations similar to Matz et al. (2018) over two burn-in periods. The first period allows creation of a genetic stock at equilibrium with no warming by simulating 100 generations of 10,000 corals under stationary sea surface temperature. At initialisation, quantitative trait loci are created by generating random values following a normal distribution (mean=0, SD=σ). As in Matz et al. (2018), thermal tolerance is assumed to be an expression of two alleles of 10 loci, so that 20 loci are assigned to each coral at random. The associated Topt is calculated by adding a normally distributed scalar (mean 0, SD=esd) to the breeding value (sum of the 20 loci). At each generation step, sea surface temperature fluctuates randomly (mean 0, SD=0.025) and fitness of all coral individuals is calculated from the difference between Topt and sea surface temperature. Fluctuating temperatures affect coral reproduction: gamete production is proportional to fitness with perfectly fit corals producing a maximum 100 gametes. Each gamete is created through a random selection of 10 of the 20 parental loci, with mutations occurring at a rate of 1*e*-six per locus. A mutation results in the addition to the muted locus of a scalar generated from a normal distribution (mean 0, SD=0.2) (Matz et al. 2018). Fertilisation occurs through the random selection of two gametes given they come from different parents (i.e. self-fertilisation is not allowed) and leads to the creation of a new phenotype. At each generation, 10,000 new genotypes are created to maintain constant population size. At the end of the equilibration period, another 100 generations are simulated with sea surface temperature increasing at a rate of 0.05°C per generation (~0.1°C per decade, assuming a coral generation represents ~ five years, Matz et al. 2018) in order to obtain a genetic pool of quantitative trait loci pre-adapted to warming.

Initialisation of demographic simulations

Demographic simulations start with the creation of coral colonies of different sizes (i.e. circular areas in cm^2) following a lognormal distribution, so that the total area of live coral matches the input value of proportional cover for each coral species. Coral colonies are randomly dispatched over the grid and assigned a genotype randomly selected from the local pool of quantitative trait loci. Phenotypes are then computed as breeding value plus the Gaussian distributed noise plus the mean sea surface temperature calculated for each reef over the past 10 years, assuming this represents the average value of Topt across the population. Corals keep the same Topt during their entire life and thermal tolerance is expressed by separating responses to chronic temperature fluctuations (mean annual sea surface temperature) and to episodes of marine heatwaves (degree heating weeks). This allows for the simulation of the evolutionary dynamics of corals through the combined ‘soft’ and ‘hard’ selection of thermal tolerance. Processes underlying a soft selection involve colony growth and fecundity as an expression of coral fitness. Hard selection is achieved through resistance to bleaching, with coral survival being dependent on degree heating weeks values relative to Topt.

Coral fitness in response to fluctuating sea surface temperatures

At every time step, thermal fitness is evaluated for each coral by calculating the difference between Topt and the mean annual sea surface temperature of the reef, with thermal fitness declining away from Topt for warmer and colder temperatures. A drop-in fitness reduces growth and fecundity proportionally. Available experimental evidence is quite limited for a robust parametrisation of the shape of this curve across the full range of temperature fluctuations (Fig. 41A,B). As a first approximation, one can assume coral fitness follows a Gaussian curve (Matz et al. 2018) so that change in fitness is symmetrical when temperature moves away from Topt on the warm and cold sides. An important parameter is the standard deviation σ of this Gaussian curve as it determines the breadth of thermal tolerance. While σ is likely to vary among coral species, the existing data are limited and somewhat conflicting, leading Matz et al. (2018) to explore a range of values from 0.5 to 2 corresponding, respectively, to a fitness drop of 86 percent and 13 percent when temperature mismatches Topt by 1°C (Fig. 41C). With a limited empirical support, predicting the evolutionary dynamics of corals is challenging and requires simulating adaptation scenarios with different tolerance breadth values.

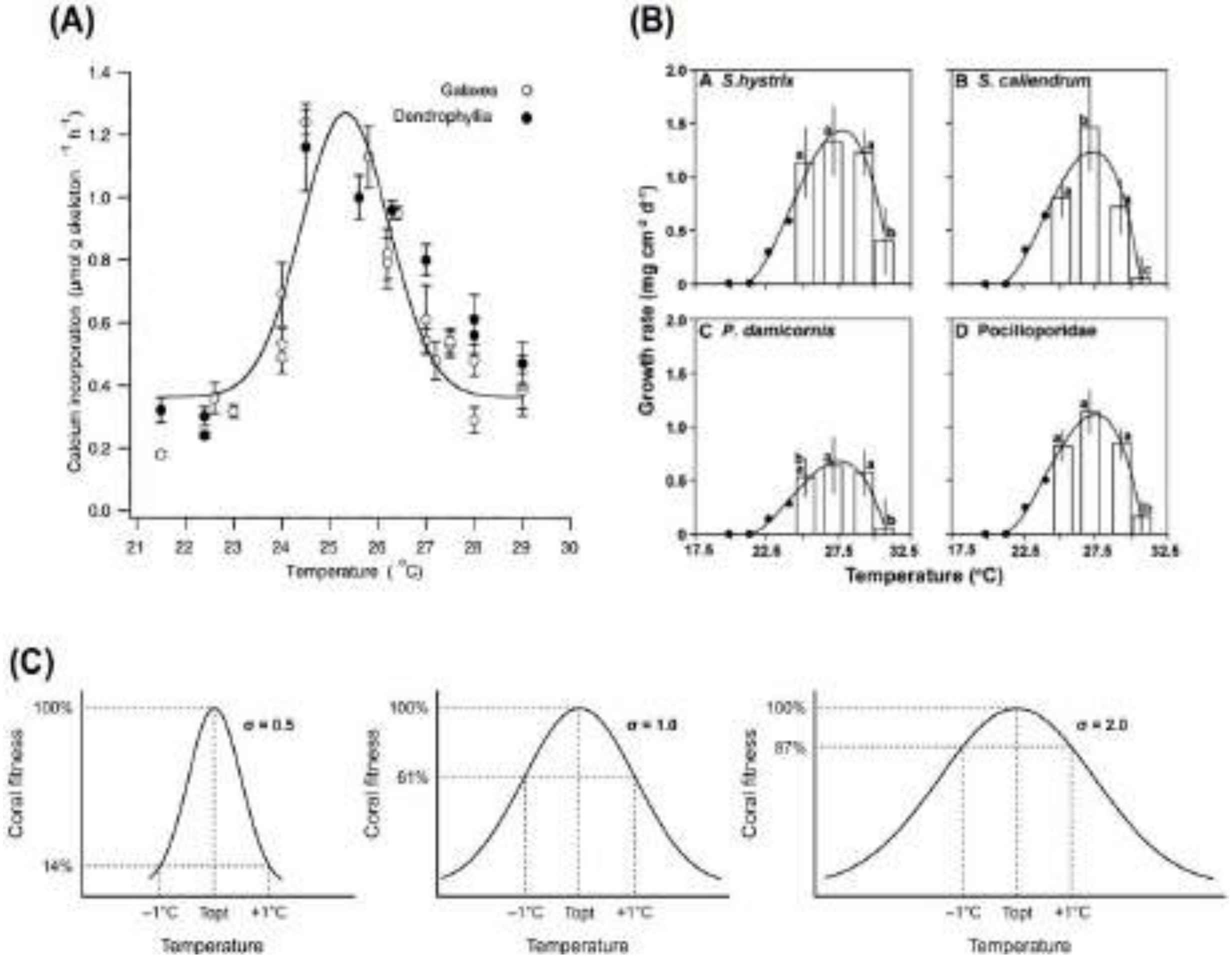


Figure 41: Experimental growth curves of corals subject to a range of temperatures (A) (Marshall and Clode 2004) at Heron Island (southern Great Barrier Reef) and (B) (Edmunds 2005) at One Tree Island (southern Reef). (C) Modelled growth curves with increasing tolerance breadth (σ) values.

While thermal fitness results in the selection of the most tolerant and well-adapted phenotypes to fluctuating temperatures, the success of adaptation to warming is also driven by the efficiency of trait transmission from one coral generation to the next. Phenotypic thermal optima are partly determined by the environmental component which modulates the genetically driven breeding value. Specifically, a strong environmental influence in the expression of thermal tolerance would imply a loose relationship between the phenotypic and genotypic compositions, pointing to a low heritability of thermal traits. Following Matz et al. (2018), heritability is represented by the standard deviation (esd) of the normal distribution used to generate the value of Topt from the breeding value. A null value of parameter esd implies that Topt perfectly matches the breeding value, meaning heritability is perfect; under this scenario, fluctuating temperatures might result in an efficient selection of genes that confer thermal tolerance, leading to a rapid evolution of thermal traits. Conversely, the greater the esd value the greater the chance to generate discrepancies between Topt and the breeding value, which can lead to selecting genes that are not related to the actual fitness of the coral. In this case, the evolution of thermal traits is likely to be slow, although a greater diversity of phenotypes in the population might buffer the selective pressure of increasing temperatures. As for the breadth of thermal tolerance, heritability in the form of esd is largely unknown for corals so that different values must be considered as possible evolutionary scenarios. Matz et al. (2018) explored the dynamics of coral adaptation with esd = 0 (perfect heritability) and esd = 2 (low heritability) which is considered here as the upper and lower bounds of heritability of thermal tolerance in the absence of empirical support.

B2.1.12 Coral resistance to acute thermal stress (bleaching)

The phenotypic expression of thermal tolerance also includes greater resistance to bleaching and it is assumed that sensitivity to extreme temperatures is proportional to Topt, so that warm-adapted corals have greater resistance to bleaching. Marshall and Clode (2004) measured calcification rates in polyps of two coral species, Galaxea fascicularis and Dendrophyllia sp. at Heron Island at different times of the year from 1991 to 2001. They observed a change in calcification with temperature (range 21–29°C) with a maximum calcification rate achieved at ~25°C (Fig. 42A). Monthly averages of maximum temperature recorded at Heron Island from 1995 to 2000 indicated a maximum monthly mean (MMM) temperature of ~28°C, which is approximately +3°C above the optimum temperature estimated for these two corals.

Degree heating weeks, a measure of thermal stress able to cause bleaching mortality, is calculated as the cumulative exposure to temperatures exceeding a critical threshold (Fig.42), which is currently defined as 1°C above a reference MMM (e.g. between 1985 and 1993):

$$T_{critical} = MMM_{85-93} + 1°C$$

Assuming MMM is the functional equivalent of Topt, the amount of thermal stress for a given coral X can be recalculated using a threshold that is function of the coral thermal optimum:

$$T_{critical}(X) = T_{opt}(X) + offset°C + 1°C$$

where the offset corresponds to +3°C following Marshall and Clode (2004). This offset of 3°C is assumed for any coral on any reef in the absence of information across species and latitudes. Therefore, instead of calculating degree heating weeks uniformly for all corals from the MMM of a given reef, degree heating weeks stress is estimated for every coral individually relative to its thermal optimum.

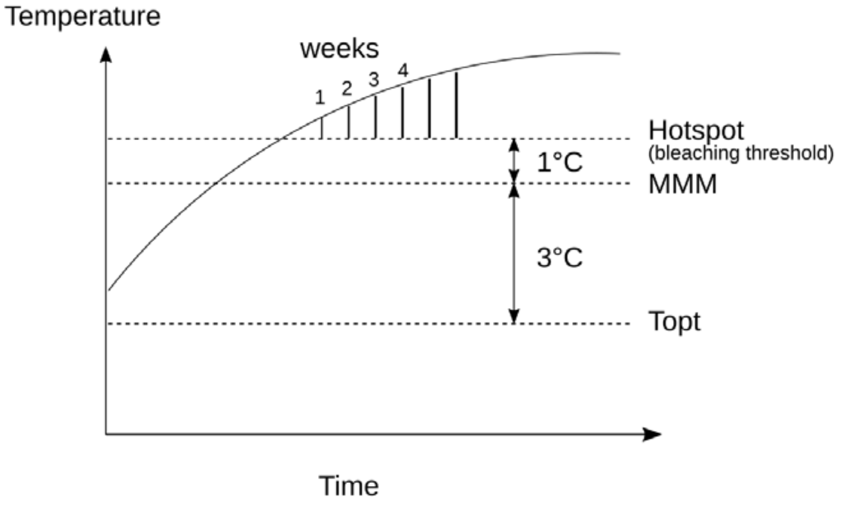


Figure 42: Principle of thermal stress (degree heating weeks) calculation as a function of the optimum temperature (Topt) of each coral.

B2.1.13 Gene transmission through sexual reproduction (mass spawning)

After each reproductive event, a pool of 1000 genotypes representative of the QTL composition of coral offspring is created for every reef. These genotypes are generated through the random sampling of coral parents where the probability of sampling is proportional to thermal fitness and the number of offspring produced by each coral. As a result, corals with a Topt close to the ambient temperature are more likely to pass their genes to the next generation. To reflect the genetic diversity of a given source reef, mutation rate is elevated proportionally to reef area, so that larger reefs have a greater diversity of genotypes due to a greater incidence of genetic mutation. The pools of larval genotypes are used to determine the genetic composition of coral recruiting on a sink reef. Every successful settler is assigned a genotype by sampling randomly across all the larval genetic pools of donor reefs, with a probability of sampling that is proportional to the contribution of each source reef to larval supply.

B2.1.14 Model outputs

For a given set of parameter values, multiple runs are required to capture the variability resulting from stochastic mortality and spatial interactions. Model outputs include the cover of the six coral groups every six months averaged across multiple replicate simulations, but also the density of coral recruits, juveniles and adults for different size classes in every reef of the Reef, the size distribution of each coral population, the average cover of turf and macroalgae, the average cover of rubble and average crown-of-thorns starfish density at every reef. Mortality events are tracked through coral cover loss associated with each stressor. In addition, estimates of the genetic and phenotypic (thermal optimum) diversity are available at a reef-by-reef scale. Importantly, the model simulates a level of uncertainty associated with the predicted reef state. Some of that uncertainty stems from stochastic processes such as cyclones, flood events, thermal anomalies. Parts of this uncertainty is artificially inflated because of the use of random values for initial coral cover at different reefs. As a result, model outputs (averages) are be accompanied by their coefficient of variation determined from replicate simulations.

Quantitative relationships can predict the quality of coral habitats (e.g. for fish) from the predicted community states, and, ultimately, fish productivity for reef valuation. A first approach uses field observations on reef structural complexity and coral community composition collected in Indonesia by Rogers et al. (2018). In this study, physical refuges of different sizes were counted on four replicate 10m×1m transects laid on 16 reef sites. Refuges were defined as any hole or crevice within the reef framework that offers physical protection to fish, including spaces within corals, between corals of different growth forms and underneath various overhanging structures. Two kinds of refuges were assessed:

Refuges within stands of branching corals; their density was estimated indirectly by measuring the area of branching colonies (length×width) assigned to either fine (1cm-2.5cm) or medium branching (2.5cm-5cm) space. Assuming an average branching coral consists of 2/3 branches and 1/3 branch space (estimated from image analysis), colony area was converted into refuge density by dividing the total branch space by the maximum branch space. The resulting metric is density of fine and medium branching refuges per site. For refuges outside stands of branching corals; their density was measured by sticking fish models of different size (5cm increments) inside holes and crevices of the reef framework made of dead carbonate and living non-branching corals (massive, encrusting, foliose, sub-massive and *Pocillopora*). The resulting metric is density of refuges per size class per site.

Because the two metrics relate to different substrata (branching and non-branching), separate relationships can be derived to estimate the density of refuges from benthic cover data.

For the 14 sites where branching colonies have been surveyed, we determined the relationship between the cumulative density of refuges within fine and medium branching corals and the percent area covered by these colonies along the 10m transects (Fig. 43A):

$$R_{Branching} = 4.596 + 6.241 \text{ percent branching}$$

For the 16 sites, the cumulative density of all refuge sizes measured outside branching corals was related to the percent area covered by non-branching corals (Fig. 43B). Because benthic composition for non-branching corals was not estimated on the 10m x 1m transects, we used nearby assessments performed online-intercept transects:

$$R_{NonBranching} = 1.468 \text{ (percent non-branching) } ^\wedge\ 0.878$$

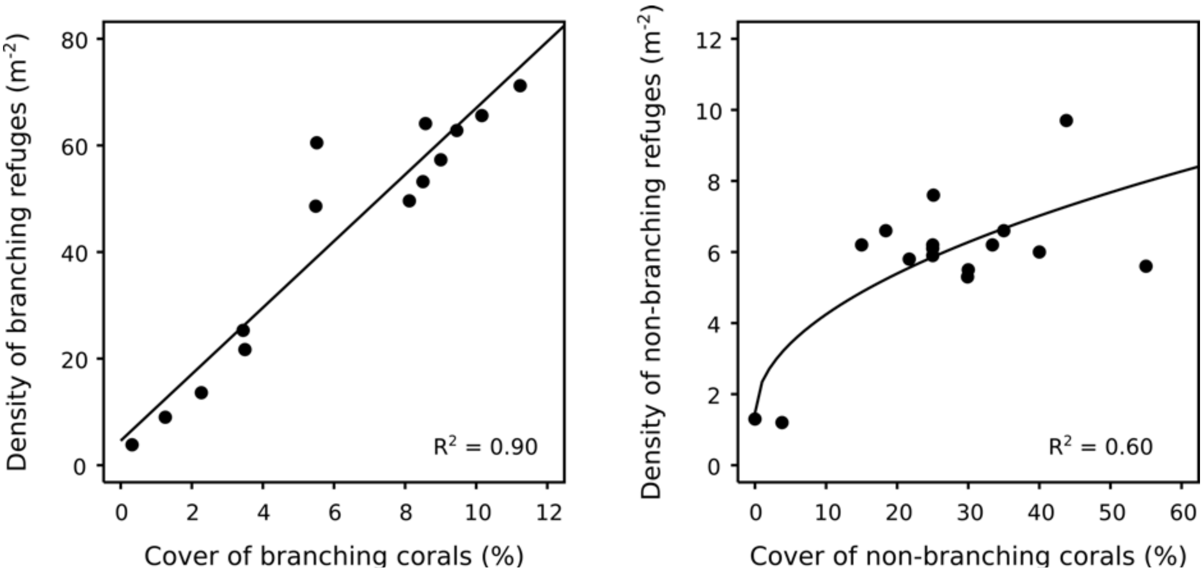


Figure 43: Empirical relationships between refuge density and the cover of branching and non-branching corals

With these two relationships we can obtain rough estimates of refuge density from the cover of branching Acropora and the cover of all other corals predicted by ReefMod. Once a value of structural complexity (refuge density) is assigned to a reef, we can further infer fish productivity and biomass following Rogers et al. (2018) model predictions (Fig. 44):

Fprod = 22.214 + 0.610 R – 0.009 R2
Pbiom = 23.873 + 1.614 R – 0.014 R2
with R = RBranching + RNonBranching

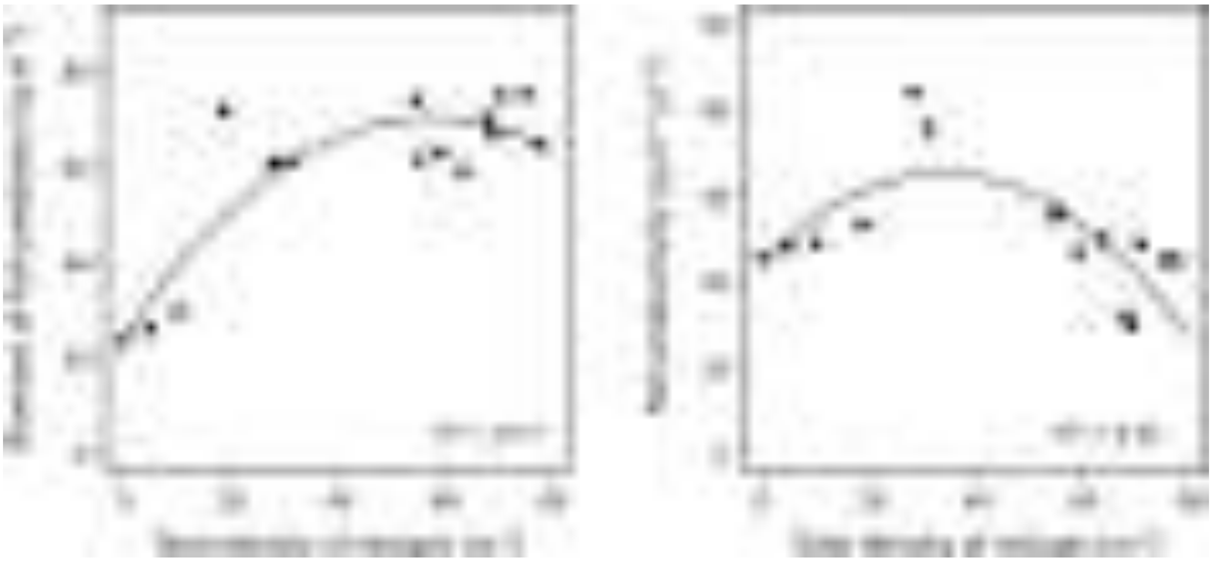


Figure 44: Estimates of fish productivity and predator biomass from a size-based ecosystem model (Rogers et al. 2014) for the refuge density estimated in Indonesia (modified from Rogers et al. 2018). Blue dot = ecosystem model's expectation with no refuge.

This approach has limitations. First, the functional impact of tabular corals is not captured because these corals were rarely encountered during Indonesian field surveys. Moreover, large overhangs and other crevices in excess of 50cm in length were not assessed as Rogers et al. (2018)'s model did not represent fish larger than this body size. Second, this approach gives a disproportionate weight to branching corals as they largely drive the number of refuges (Fig.43). Finally, this assumes that branching corals disappear following mortality, while dead skeletons can still provide fish habitat before structural collapse due to mechanical erosion.

B2.2 Hindcast

B2.2.1 Parameterisation

To determine the initial conditions of reef state for the forecast simulations (i.e. coral cover as in 2018), 40 replicate simulations were run with spatially and temporally realistic regimes of water quality, crown-of-thorns starfish, bleaching and cyclones between 2008 and 2017 (10 years).

Initial benthic cover

For each replicate simulation, the initial coral cover for a given reef was randomly generated from a normal distribution centred on a predefined average (standard deviation: 10 percent). Average coral cover at the initial step was derived from data collected by the AIMS Long-term Monitoring Program in 2006-2007. This dataset provided reef-wide coral cover for more than 80 reefs across the entire Reef. The other reefs were initialised with the mean coral cover reported for each management sector and shelf position (inner-, mid- and outer-shelf reefs). Initial total coral cover for all reefs was distributed among the 6 functional groups following rough average community composition reported by AIMS Long-term Monitoring Program on the inner-, mid and outer-shelf reefs. The cover of rubble and ungrazable substratum (i.e. sand) are randomly generated from a normal distribution with mean 10 percent and standard deviation 10 percent.

Water quality regime

Water quality regime and impact on coral demographics during 2008–2017 was reproduced by selecting at every time step a spatial layer of coral reproduction success, recruit survival of Acropora corals and juvenile growth representative of the 2011–2016 regime of suspended sediments. The missing years were completed with the available layers assuming the period 2011–2016 is roughly representative of a cycling regime of rainfall, river flow and sediment transport across the Reef. Inter-annual variability was maintained by imposing the 2014–2016 seasonal layers to the simulated period 2008–2010, and the 2011 layers to the simulated year 2017.

Exposure to crown-of-thorns starfish outbreaks

Exposure to crown-of-thorns starfish outbreaks during 2008–2017 was reproduced by combining observational data with demographic simulations for reefs where no field observation was available. Manta tows from the Great Barrier Reef Marine Park Authority's Field Management Program (FMP) and AIMS Long-term Monitoring Program were used to inform crown-of-thorns starfish population densities on ~6 percent of all reefs (242 out of 3,806 reefs). This led to exposure layers with indicator values of -1 (no observation available), 0 (no outbreak detected), 1 (incipient outbreak) and 2 (active outbreak). At initialisation, reefs not surveyed and reefs with no detected outbreak were set with a null density of crown-of-thorns starfish. Reefs with incipient and active outbreaks were initialised with the median values of crown-of-thorns starfish densities reported by FMP manta tows (respectively 2075 and 7450 adult crown-of-thorns starfish per km^2, roughly equivalent to 0.3 and 1.1 adult crown-of-thorns starfish per tow, Moran and De'Ath 1992). For outbreaking populations, density-at-age (six-month classes) was generated from reference age distributions as determined by the demographic model underage-specific mortality and constant recruitment, assuming incipient and active outbreaks have been developing, from scratch, for three and five years respectively. Density-at-age was corrected for imperfect detectability using empirical predictions from MacNeil et al. (2016). At the following steps, crown-of-thorns starfish populations on reefs that were not surveyed in a given year were estimated by the model based on standing populations and larval connectivity, while reefs surveyed that year were imposed the corresponding reference population (i.e. absent, incipient or active outbreaking described above) in such a way that preference was always given to field observations.

Exposure to thermal stress

Past degree heating weeks records for the 3806 reefs were derived from Hock et al. (2017) which combines satellite data from the Coral Reef Temperature Anomaly Database (CoRTAD version 5) for years prior to 2012 (Casey et al. 2015) and data from ReefTemp Next Generation (Garde et al. 2014). The reconstructed regime of thermal stress captures the most recent (2016-2017) bleaching events.

Exposure to cyclones

Spatially explicit hindcast of exposure to cyclone was generated from sea-state predictions of wave height (Puotinen et al. 2016). The potential for coral-damaging sea state (wave height >4m, Puotinen et al. 2016) was determined using a map of wind speed every hour within 4km pixels over the Reef for cyclones between 2008 and 2017. Any areas containing a combination of wind speed and duration capable of generating 4m waves, assuming sufficient fetch, were scored as positive for potential coral-damaging sea-state in the respective year. For each year, occurrence of damaging wave height was interpolated to the 3806 reefs, and where damaging waves were predicted to occur, coral mortality was estimated from the cyclone category (Saffir-Simpson scale) derived from the closest estimate of maximum mean along the cyclone track as provided by the Database of Past Tropical Cyclone Tracks of the Australian Bureau of Meteorology.

Outputs: coral condition in 2018 across the entire Reef and in the Cairns region

An overall view of present-day coral conditions across the entire Reef, as estimated from hindcast (2008–2017) simulations, is presented on Fig 45. This picture includes cover predictions for the six coral groups for 3806 reef polygons. The reef surface associated to each reef polygon was derived from the indicative reef outline (~0m-10m) provided by the Great Barrier Reef Marine Park Authority data on the Reef boundaries (Great Barrier Reef Marine Park Authority 2007).

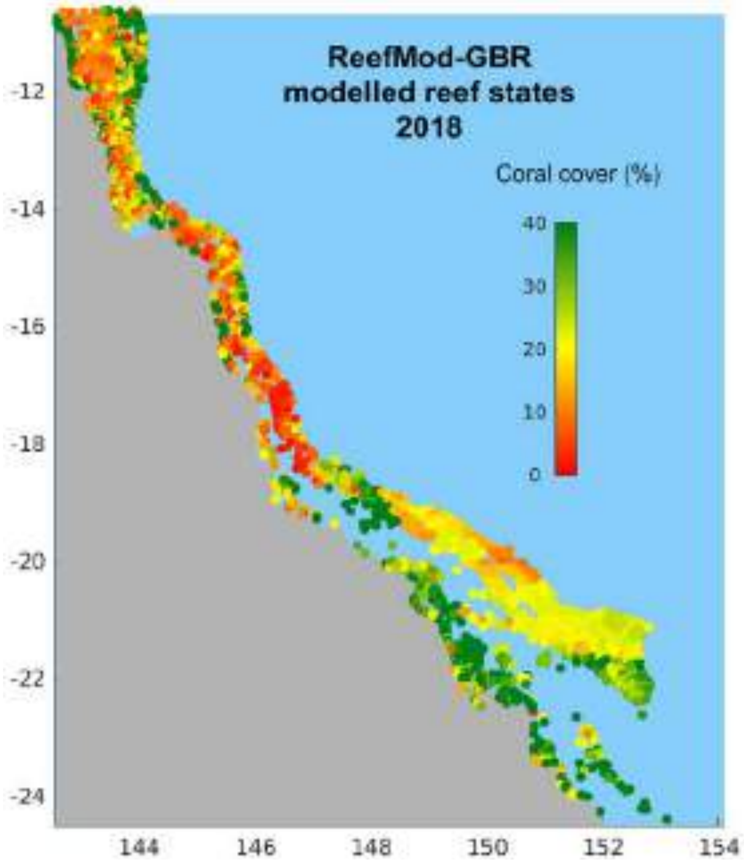


Figure 45: Result of hindcast simulations leading to the estimate of present-day (2018) coral condition (total coral cover) across 3806 reefs of the Great Barrier Reef.

A focus on the Cairns section is presented on Fig. 46 as this region benefits from recent high-resolution habitat mapping (C. Roelfsema, The University of Queensland). This mapping product is derived from satellite imagery and an object-based analysis for defining geomorphic zonation and bottom type (Roelfsema et al. 2018). At the start of the RRAP Concept Feasibility Study, the geomorphic maps were only available for the Cairns Management Area. Because they offer more precise estimates of reef surface areas, which is critical for estimating the deployment cost of many RRAP interventions, they were used for all the forward projections of coral condition (counterfactuals and interventions) presented hereafter. As a result, the benefits of RRAP interventions were only assessed on the Cairns section of the Reef. Since ReefMod is parameterised with coral demographic rates representative of a mid-depth (~5m–10m) reef environment, we only selected the reef slope habitat (3m-10m depth) as the modelled surface for every reef, leading to the selection of 156 reefs that exhibit a total reef slope area >0.17km^2.

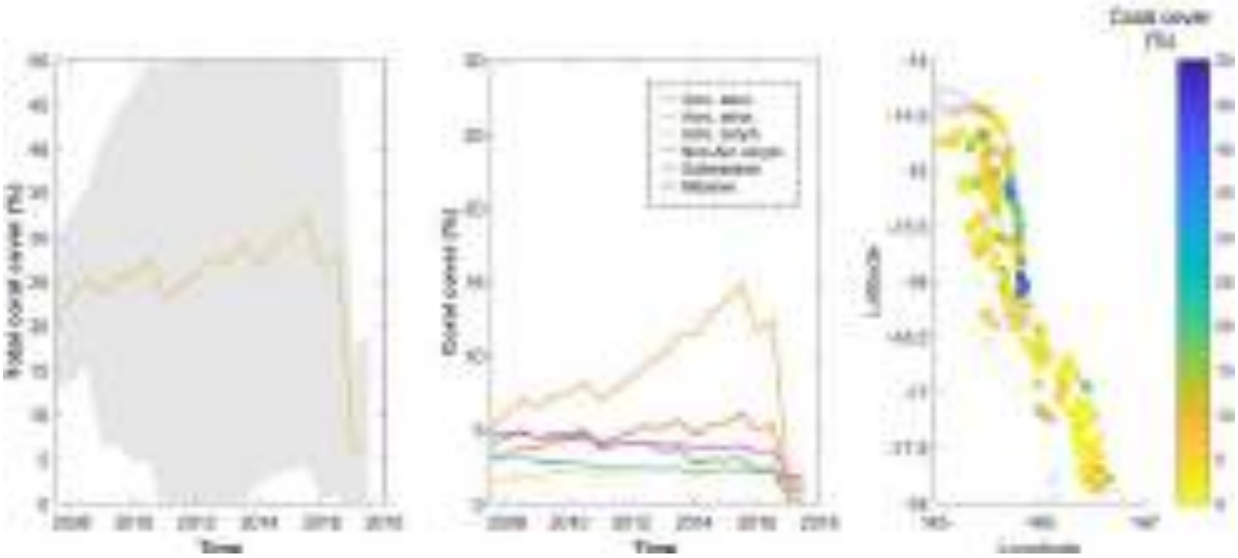


Figure 46: Hindcast reef trajectory in the Cairns region. (A) Averaged trajectory (orange) of the 156 reefs with a 90 percent confidence envelope (grey), calculated from the mean and variance (over 40 replicate runs) of the regionally averaged total coral cover weighted by reef areas. (B) Averaged trajectory of the six functional groups; (C) Map of the current (2018) state of the 156 reefs as predicted by the model.

Validation of these hindcast simulations is still in progress. To determine the extent to which ReefMod-GBR can predict coral cover in changing environments with confidence, model predictions will be compared against the coral trajectories monitored by AIMS Long-term Monitoring Program for the period 2008 to 2017. We anticipate some discrepancies between observed and predicted reef state because location-specific disturbances may not be captured by our model parameter values. Some habitats may unexpectedly escape cyclone/crown-of-thorns starfish/bleaching damages and some habitats may have been impacted by disturbances that went undetected (including coral disease). Also, crown-of-thorns starfish control was not included in these hindcasts. As the model develops further and local processes are captured and used to continuously update and calibrate model functions, we expect that the predictive capacity of ReefMod will improve over time. For the purpose of the RRAP Concept Feasibility Study, these estimates of coral condition across the Cairns section must be considered as tentative predictions under specific assumptions of past stress exposure.

B2.2.2 Forecast: counterfactual scenarios

Forward projections (2018-2070) of coral cover under climate change were performed for the Cairns Management Areas from the coral condition estimated for each group by the hindcast simulations. This region includes Cooktown-Lizard Island, Cairns and Innisfail Management Areas and is represented by 156 individual reefs as defined by the most recent mapping of reef habitats.

Forward projections of reef water quality were obtained by repeating the 2011–2016 regime of suspended sediments in the same chronological order, from 2018 to 2070. Exposure to crown-of-thorns starfish outbreaks was simulated using forecast predictions of the CoCoNet model under the two warming scenarios RCP 2.6 and RCP 8.5 and a business-as-usual control effort (8 control vessels). CoCoNet forecast simulations provided mean and standard deviation of crown-of-thorns starfish per manta tow across the Reef (2096 reefs), based on the selection of 50 model runs that all had <12 percent average coral cover in 2018, which is assumed to be representative of reef states within the Cairns region as predicted by ReefMod. The time series were interpolated to the 156 reefs. At every time step on a given reef, a number of crown-of-thorns starfish per tow is generated from a normal distribution using the mean and SD predicted by CoCoNet for that particular reef and year, and converted into an equivalent density for the crown-of-thorns starfish population relative to the area of the reef (assuming 0.22 crown-of-thorns starfish per tow represent 1500 crown-of-thorns starfish per km^2, Moran and De'Ath 1992). Crown-of-thorns starfish population density was disaggregated per age class using the reference age distribution of an outbreaking population (see section Hindcast) and corrected for imperfect detectability using empirical predictions from MacNeil et al. (2016).

Forward projections of sea surface temperature and thermal stress followed the methodology developed by Wolff et al. (2015, 2018). First, future climatology was derived from the UK Hadley Centre Global Environmental Model HadGEM2-ES following two scenarios of greenhouse gas emission and concentration: the representative concentration pathways (RCP) 2.6 and 8.5, which, respectively, predict a global warming of 1°C and 2.2°C by the end of the 21st century. The coarse (1×1° resolution) Hadgem RCP sea surface temperature trajectories were adjusted to every reef based on the difference between past (1985–1993, omitting '91 and '92) Hadisst (1×1°) and CoRTAD (4km×4km) climatology. By using this approach, each CoRTAD pixel has an associated Hadgem trajectory without altering the warming trends. The 3806 reef centroids were intersected with CoRTAD pixels to produce reef-by-reef projections of sea surface temperature.

To predict thermal stress, a maximum monthly mean temperature was calculated for each reef based on the CoRTAD 1985–1993 (omitting '91 and '92) climatology. Future monthly anomalies >1°C above the maximum monthly mean from the climatology were accumulated within a three-month window to calculate degree heating months. Degree heating months were converted into degree heating weeks by multiplying by 4.3 (weeks per month).

If all individuals of a specific coral species were assumed to have the same thermal sensitivity, thermal stress would be estimated by using a reference threshold (maximum monthly mean +1°C) above which temperature anomalies accumulate (Wolff et al. 2015, 2018). Here, thermal stress is assumed to be dependent on coral's optimum temperature of individual corals, so that calculations must consider temperature anomalies above different thresholds (Topt +4°C). Reef-specific thermal stress values were then calculated for a range of Topt values varying from 15 to 40°C by increments of 0.1°C. Specifically for each reef climatology, future monthly anomalies >4°C above each Topt value were accumulated within a three-month window to calculate Topt-specific degree heating months were converted into degree heating weeks (by multiplying by 4.3) for the two RCPs (2.6 and 8.5). This way, a risk of mortality specific to each coral (relative to their Topt) can be calculated for a particular reef and year.

Forward projections of cyclone exposure were based on recent (1970–2011) cyclone tracks following the methodology developed by Wolff et al. (2016). Briefly, reef-scale probabilities of a cyclone occurrence were estimated from the annual rate and clustering statistics for each reef polygon. These statistics were used to generate 100 regional-scale cyclone disturbance regimes (simulations) for the period 2018–2070. When a cyclone event occurred within a reef polygon for a given simulation/year, a cyclone was randomly selected from a pool of 7000 synthetic tracks associated with that grid cell (see details in Wolff et al. 2016). Finally, whether a model reef was impacted by a particular cyclone occurring within its grid cell depended on the path of the cyclone and the extent of its damaging winds. Each track was disaggregated into cyclone categories 1–5 on the Australian Bureau of Meteorology scale based on maximum sustained circular winds. A buffer was applied to each category track using wind speed extents defined by Keim et al. (2007) and a method described in detail in Edwards et al. (2011). The approach was adjusted to the Southern Hemisphere (opposite storm wind extent asymmetry to northern hemisphere) and the differences between the Australian Bureau of Meteorology and Saffir–Simpson hurricane classification system. Model reefs were intersected with buffered cyclone tracks to determine which cyclones affected each reef and the category of wind they experienced. Because there is no overlap between the 1970–2011 database of cyclone tracks and the 2011–2016 water quality regime, the projected forcing of suspended sediment and chlorophyll concentrations is unrelated to the projected storm events.

Actual adaptation rates are uncertain with a wide range of possible values of heritability and thermal tolerance. While the parameter space of thermal adaptation will be fully explored in the RRAP R&D Program, only two adaptation scenarios were considered here by using the credible lower and upper bounds of thermal tolerance and heritability:

- A **low adaptation potential** whereby corals have a somewhat narrow thermal tolerance ($\sigma = 1$, implying a 39 percent drop in coral fitness when temperature mismatches Topt by 1°C, see Fig. 41C) with a low efficiency of trait transmission (esd = 2).
- A **high adaptation potential** whereby corals have a broad thermal tolerance ($\sigma = 2$, implying a 13 percent drop in coral fitness for a 1°C mismatch, see Fig. 41C) with strong heritability (esd = 0.5).

For the two warming scenarios, 40 model simulations were run to estimate an average trajectory for each of the 156 reefs of the Cairns region.

Model runs show significant outcome improvements between the low and high adaptation potentials under RCP 2.6 (Fig. 47). The mean coral cover across the Cairns region exhibits an upward trajectory following the 2017 bleaching event, indicating persistence in the long term. Outcomes are significantly greater under the optimistic scenario of thermal adaptation, although forward projections of coral cover (~15 percent coral cover on average by 2070) remain well below the hindcast pre-2016-17 bleaching reef states (~25 percent coral cover on average). Thus, while it seems there is scope for thermal adaptation and long-term persistence under a scenario of aggressive reductions of greenhouse gas emissions, model projections indicate that reefs in the Cairns region might remain in a poor state for decades (i.e. below 10 percent on average).

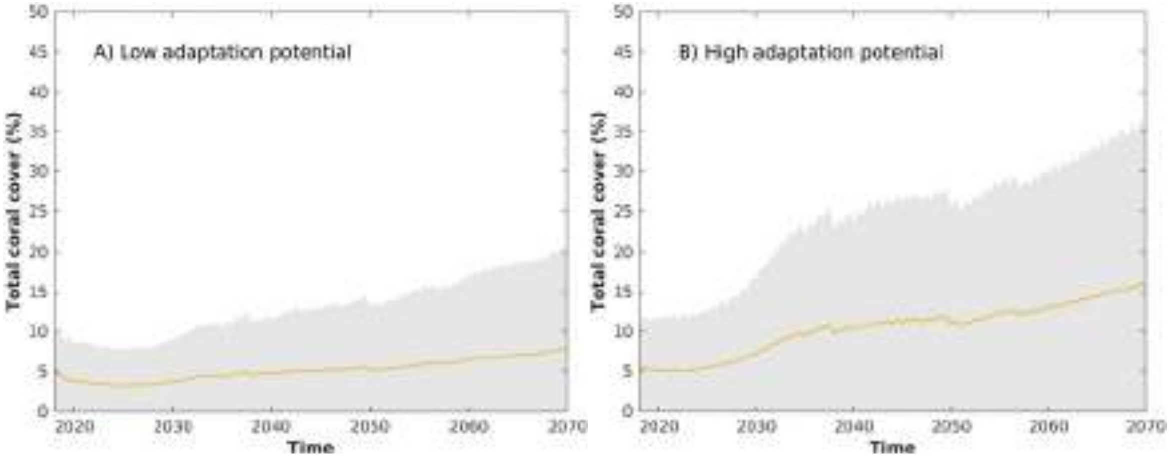


Figure 47: RCP 2.6 averaged trajectory (orange) of the 156 reefs in the Cairns region with a 90 percent confidence envelope (grey), calculated from the mean and variance (over 40 replicate runs) of the regional mean total coral cover weighted by reef areas.

Under a business-as-usual scenario of greenhouse gas emissions (RCP 8.5), the potential for thermal adaptation is impaired (Fig. 48). Under a low adaptation potential scenario, reefs in the Cairns region remain below 10 percent (~ five percent average across the region) throughout the modelled timeframe. Under a scenario of high adaptation potential, reefs seem to cope with the increasing regime of thermal stress until the middle of the century but fail to achieve persistence in the long term. The model suggests there is no scope for adaptation under business-as-usual greenhouse gas emissions.

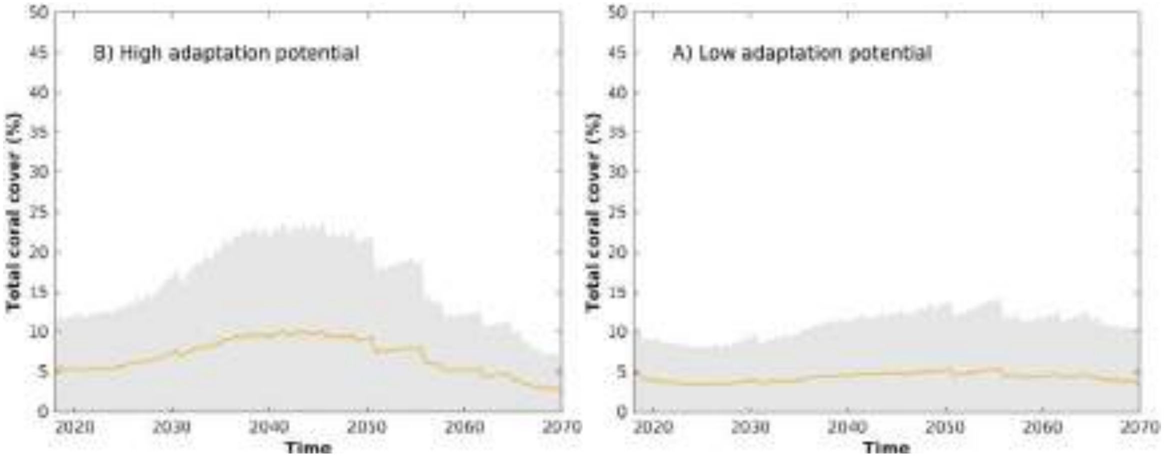


Figure 48: RCP 8.5 averaged trajectory (orange) of the 156 reefs in the Cairns region with a 90 percent confidence envelope (grey), calculated from the mean and variance (over 40 replicate runs) of the regional mean total coral cover weighted by reef areas.

B2.3 Forecast: RRAP interventions

B2.3.1 Outplanting of coral juveniles

As a spatially explicit, individual-based model, ReefMod is an efficient simulation tool to explore the performance and ecological benefits of outplanting coral individuals on the reef. Different strategies of coral deployment can be explored, whereby strategies refer to the use of different sizes (diameter) of corals (as nubbins, juveniles or adults), different densities of coral outplanting, the number of restored reefs given their size and available amount of coral outplants, but also environmental characteristics that are likely to influence the success of the intervention at local (e.g., larval retention, water quality and exposure to acute stress) or regional scales (e.g. importance of the selected reef for supplying coral larvae to other reefs).

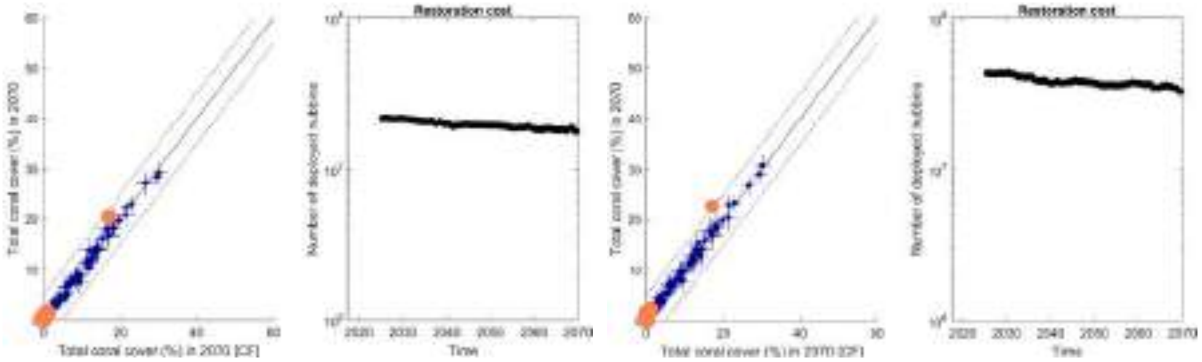
Coral outplanting was modelled as the addition of 2cm coral juveniles of plating and corymbose *Acropora* on a reef grid (400m^2). Corals were deployed once a year from 2025 onward at two densities: 0.5 and 1.0 coral juveniles per square metre. On a reef grid, the deployment is performed cell-by-cell following a stochastic process: the actual number of outplanted corals in a cell is determined at random following a Poisson distribution with the density of deployment as parameter. This number can be reduced following the current cell occupancy, with every cell being imposed a maximum 40 colonies per species. In addition, a cell cannot receive more than five coral juveniles. The genotype of deployed corals is created from the local pool of genes so that genetic diversity among the outplants reflects that of the native population. Thermal tolerance of outplants can be artificially increased by shifting their thermal optimum to warmer temperatures to simulate the outplanting of naturally or engineered warm-adapted corals. This is achieved by adding to the 20 quantitative trait loci of each outplanted coral 20 trait values selected at random, so that the breeding value elevates to the desired target (i.e. +1°C, +2°C). The model tracks the total number of corals effectively deployed across the 400 grid cells, which is scaled up to the representative habitat area of the reef, assuming for simplicity that the entire reef area is restored at the selected deployment density.

Simulations were performed for an increasing number of reefs in the Cairns region (i.e. 10, 20, 40, 60, 80 reefs out of 156) but only results for 10 and 20 restored reefs are presented since this deployment strategy required the production of a considerable amount of coral juveniles (between 20 and 80 million every year) yet the Cairns region represents only a small proportion of the Reef (~11 percent based on the area of 3806 reference reef polygons). The best donor reefs (i.e. reefs with the greatest number of larval connections with downstream reefs, referred as priority reefs) were selected assuming that local demographic benefits of coral outplanting may cascade through the network of larval connectivity. If a restored reef achieves a minimum 20 percent coral cover at any time step, restoration is stopped on that reef and the best donor reef down the list is selected for coral deployment. Outplanting is re-activated on priority reefs that eventually fall again below 20 percent coral cover. Ecological outcomes are assessed as the change in total coral cover for each reef at different points in time, relative to the counterfactual scenarios (two warming scenarios × two adaptation scenarios).

B2.3.2 Outplanting of coral juveniles with no increased thermal tolerance

Model runs show that the simulated densities of coral outplants (i.e., 0.5 and 1.0 coral juveniles per m^2) have relatively small effects on coral populations at the scale of a reef, and no detectable effects at the regional scale (Fig. 49-50). Local impact of coral deployment seems to be contingent on the current state of the restored reef with a very limited increase in coral cover obtained when depauperate reefs (i.e. below five percent cover) are targeted, probably a result of poor water quality (i.e. reefs with unfavourable conditions for juvenile growth). However, benefits of five to 10 percent can be achieved on some reefs if deployment occurs at relatively high densities (1.0 coral per m^2), although at this density the required amount of coral outplants (40-80 million a year) might be prohibitive. Local benefits seem to have no impact on downstream reefs, which suggests that larval supply is not significantly affected at the deployed densities.

10 restored reefs at density 0.5m^2 10 restored reefs at density 1.0m^2



20 restored reefs at density 0.5m^2 20 restored reefs at density 1.0m^2

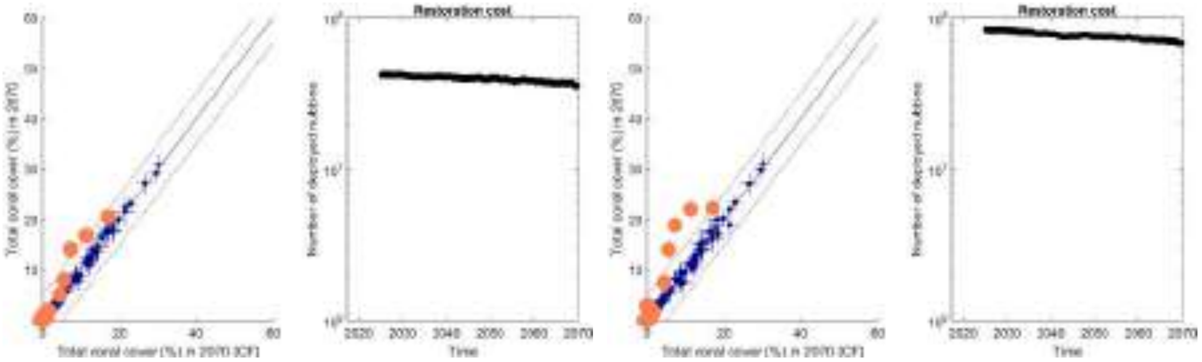


Fig.49: Long-term ecological benefits (left) and associated cost (right) of the deployment of coral juveniles across the Cairns region. Ecological benefits are measured in terms of total coral cover for the 156 reefs (dots) achieved by 2070 (y-axis) relative to the representative counterfactual scenario (x-axis). Reefs that were selected for coral deployment at least once over the simulated timeframe (i.e. priority reefs and eventual substitutes) are indicated using orange dots. Error bars indicate SD of reef coral cover over 40 replicate runs. Restoration cost is represented by the total number of coral juveniles deployed every year across the region (note the log scale) averaged over 40 runs. Simulations were performed under RCP 2.6 assuming a low potential of thermal adaptation, with deployed corals having the same thermal tolerance than native corals.

10 restored reefs at density 0.5m^2 10 restored reefs at density 1.0m^2

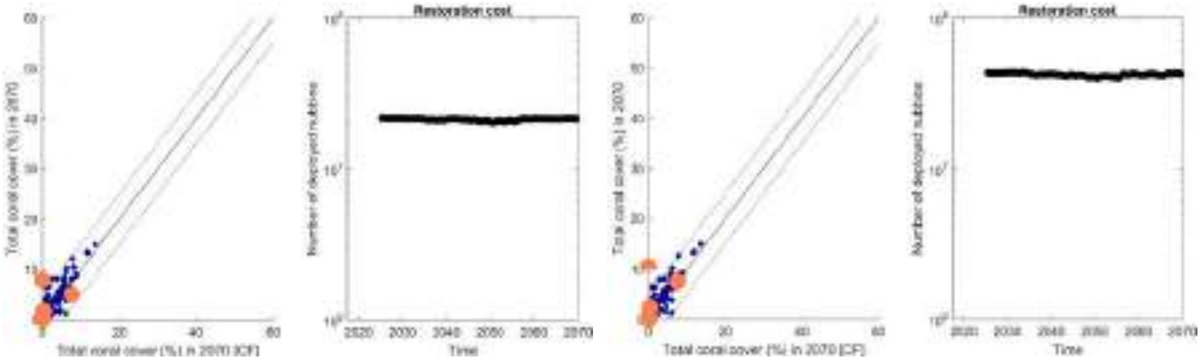


Fig.50: Long-term ecological benefits and associated cost of deploying coral juveniles with no increased thermal tolerance. Simulations were performed under RCP 8.5 assuming a low potential of thermal adaptation, with deployed corals having the same thermal tolerance than native corals.

More efficient strategies might be found by avoiding reefs with poor water quality. In addition, considering that larval supply on non-restored reef seems to be insensitive to coral deployment on reefs they are connected to, a more cost-effective approach could be to select reefs of smaller size and/or by limiting coral deployment to a portion of a reef, assuming that the non-restored portion will benefit from larval retention. It is noteworthy that reef size is absolutely key to the estimated number of coral juveniles. Here, only a specific reef habitat was considered in the simulations: the leeward and windward reef slope environment from -3m to -10m depth. While the Cairns region benefits from the most accurate account of reef habitats, using reef areas informed by the Great Barrier Reef Marine Park Authority's indicative reef polygons would have produced far greater amounts of restoration costs (Fig. 51). This highlights the need of high-resolution mapping of colonisable hard-bottom reef habitats across the entire Reef for more accurate predictions of coral deployment costs.

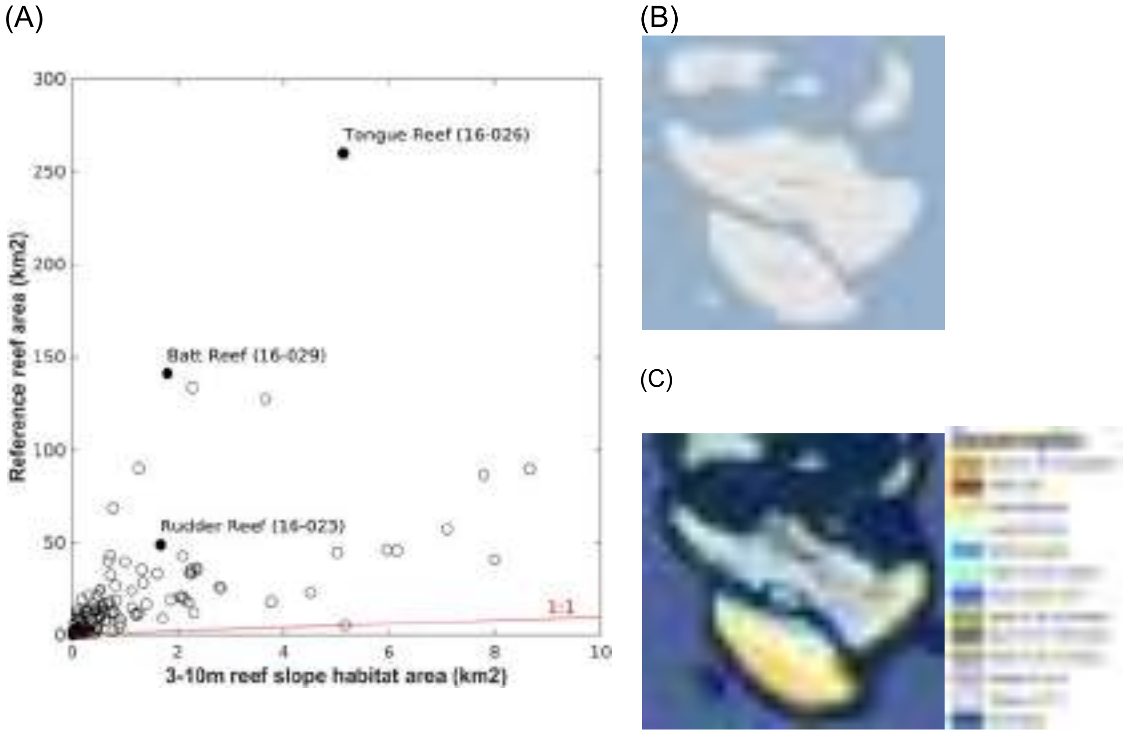
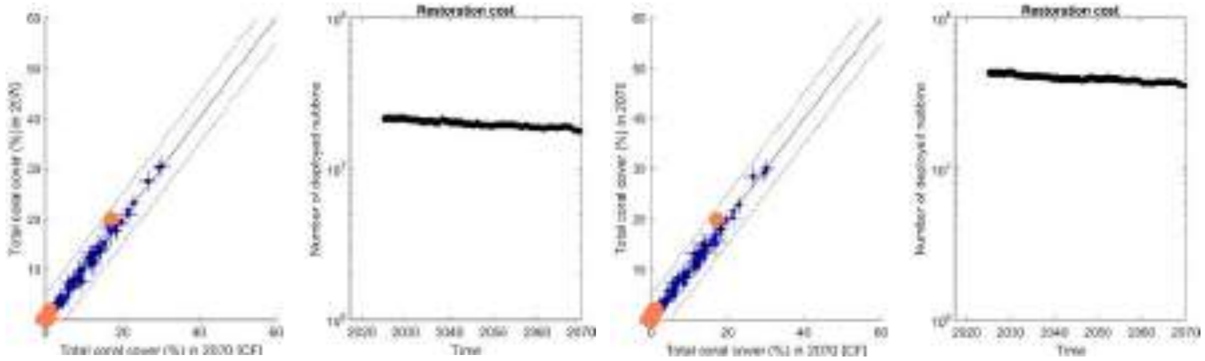


Fig. 51: (A) Relationship between the area of modelled habitat (3m-10m reef slope, only available for the Cairns region) and the reference area (Great Barrier Reef Marine Park Authority's indicative reef polygons, available for the entire GBR) for the 156 reefs. Using the reference reef areas (B) would incur restoration costs (i.e. number of coral juveniles deployed each year) on average 17 times greater than those currently estimated with the 3m-10m reef slope areas (C).

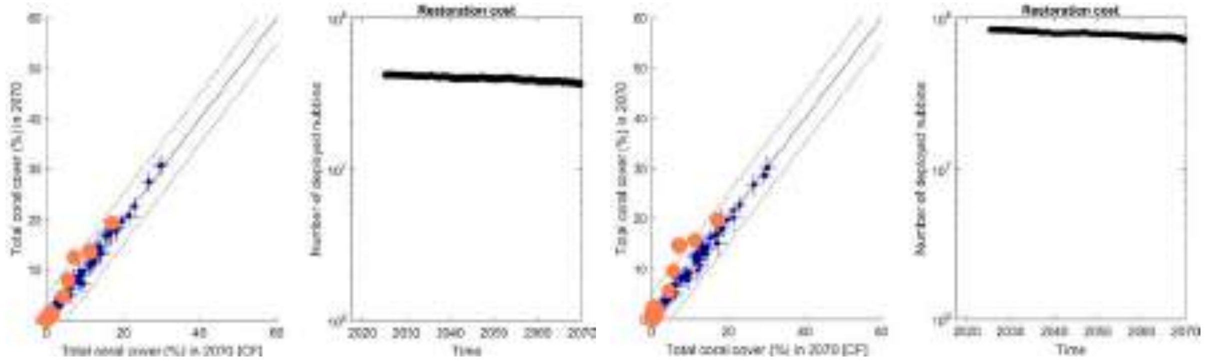
B2.3.3 Outplanting of coral juveniles with increasing thermal tolerance

Increasing the optimum temperature of coral outplants by 1°C (Fig. 52-53) or 2°C (Fig. 54-55) did not improve the outcomes of coral deployment. The simulated densities seem unable to change the composition of thermal traits across the region, despite a focus on the most connected reefs. While explanations could be the same as for the deployment of +0°C coral juveniles, another possible reason is that retention overrides external supply on those reefs. Moreover, selecting reefs that provide many dispersal routes could dilute the pool of larvae enriched with greater thermal tolerance; in this case, a more efficient strategy might be the selection of priority reefs that have fewer (yet strategic) connections to sink reefs.



10 restored reefs at density 0.5m^2

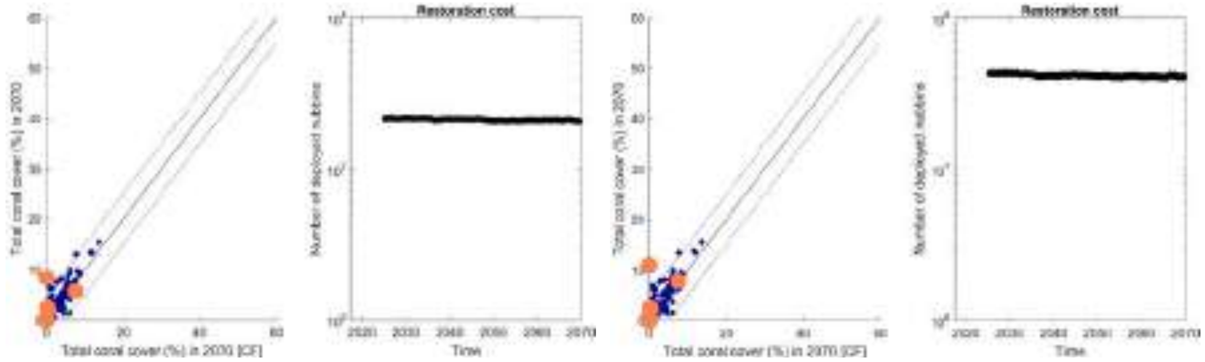
10 restored reefs at density 1.0m^2



20 restored reefs at density 0.5m^2

20 restored reefs at density 1.0m^2

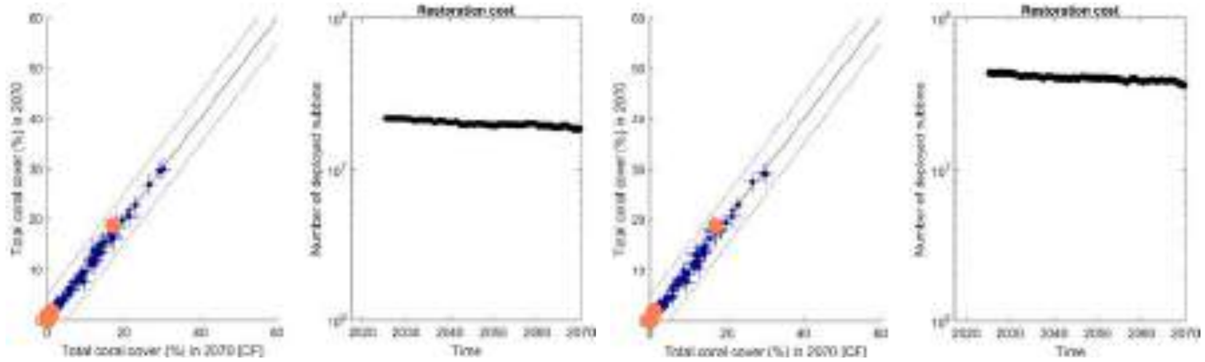
Fig.52: Long-term ecological benefits and associated cost of deploying coral juveniles with 1°C increased thermal tolerance. Simulations were performed under RCP 8.5 assuming a low potential of thermal adaptation.



10 restored reefs at density 0.5m^2

10 restored reefs at density 1.0m^2

Fig. 53: Long-term ecological benefits and associated cost of deploying coral juveniles with 1°C increased thermal tolerance. Simulations were performed under RCP 8.5 assuming a low potential of thermal adaptation.



10 restored reefs at density 0.5m^2

10 restored reefs at density 1.0m^2

20 restored reefs at density 0.5m^2

20 restored reefs at density 1.0m^2

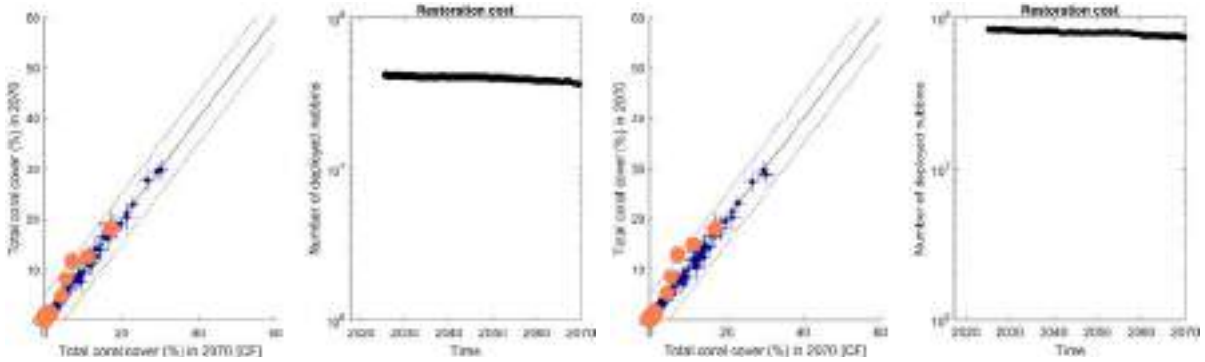
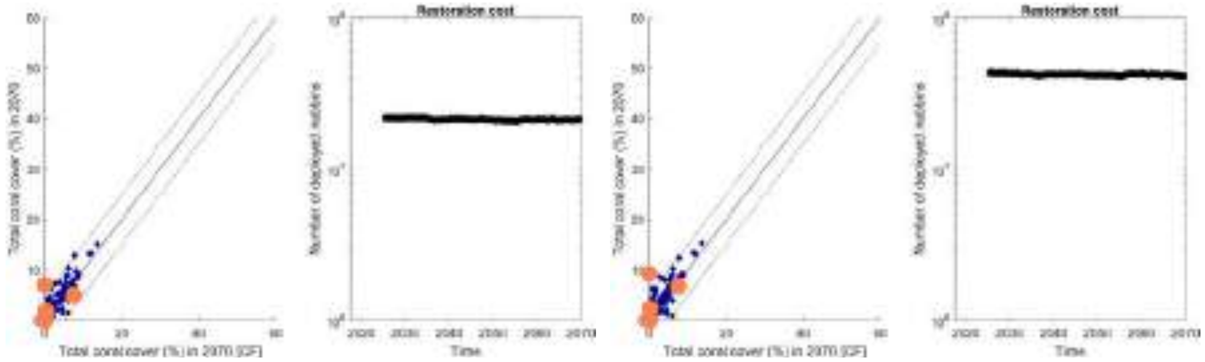


Fig.54: Long-term ecological benefits and associated cost of deploying coral juveniles with 2°C increased thermal tolerance. Simulations were performed under RCP 2.6 assuming a low potential of thermal adaptation.



10 restored reefs at density 0.5m^2

10 restored reefs at density 1.0m^2

Fig.55: Long-term ecological benefits and associated cost of deploying coral juveniles with 2°C increased thermal tolerance. Simulations were performed under RCP 8.5 assuming a low potential of thermal adaptation.

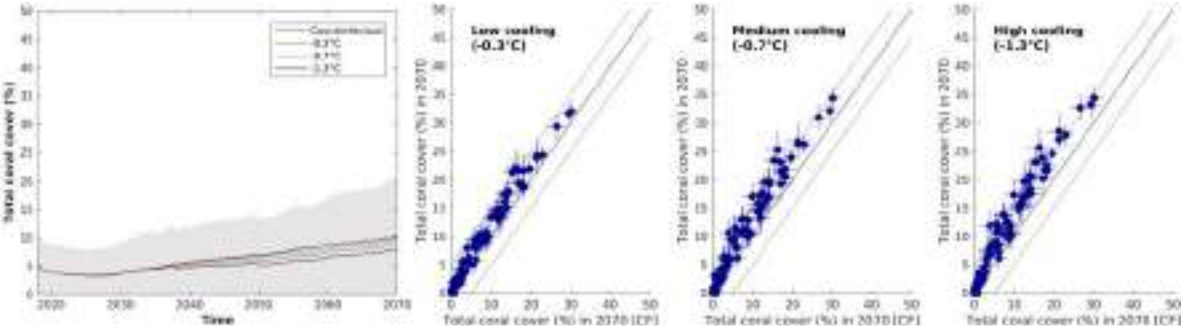
B2.3.4 Solar radiation management

Solar radiation management was simulated as a direct cooling of sea surface temperature and reduction in the severity of heat stress predicted under the two warming scenarios (RCP 2.6 and RCP 8.5). Deployment of solar radiation management was assumed to begin in 2025 and was simulated every year onward for summer steps only. Three scenarios of cooling efficiency were tested by offsetting mean annual temperatures (sea surface temperature) by -0.3°C, -0.7°C and -1.3°C for a three-month equivalent period, resulting in an altered temperature regime potentially affecting coral growth, fecundity, and, by extension, the dynamics of thermal adaptation. Reduction in cumulative heat stress was approximated by simply subtracting to the predicted degree heating weeks the cooling effect multiplied by 12, assuming solar radiation management operates over 12 consecutive weeks during the warmest summer months. This led to, respectively for the three cooling scenarios, a reduction of 3.6 degree heating weeks, 8.4 degree heating weeks and 15.6 degree heating weeks of the heat stress predicted for every increment of coral thermal optimum under each counterfactual scenario. Solar radiation management was assumed to be uniform across the Cairns region, so the same cooling effect was simulated for all reefs relative to their forecast climatology (2018-2070). Ecological benefits of solar radiation management were assessed through 40 replicate runs by comparing the regional mean coral cover with that obtained from the representative counterfactual.

Under RCP 2.6, solar radiation management has a significant impact by gradually increasing coral cover as the efficiency of cooling increases (Fig. 56). A region-wide benefit becomes apparent more than one decade after deployment and achieves a maximum five percent mean (i.e. regional average) coral cover by 2050 for the most efficient cooling effect (i.e. -1.3°C). The impact of artificial cooling is not uniform across the region with maximum local benefits around 10 percent coral cover (as estimated in 2070). Reefs exhibiting < five percent coral cover in 2070 are the least affected by solar radiation management. Ecological benefits are slightly greater under the optimistic scenario of coral adaptation.

Under RCP 8.5, solar radiation management has a greater impact with benefits for coral populations becoming apparent five years after deployment (Fig. 57). A maximum benefit of 10 percent mean coral cover is achieved under the greatest cooling efficiency, with maximum local benefits around 15 percent coral cover in 2070 including for low coral cover (i.e. <5 percent cover) reefs. The impact of solar radiation management is sensibly greater under the most optimistic scenario of thermal adaptation, with even higher benefits predicted to occur during the decade 2050–2060. These benefits, however, might not persist in the long term, as all cooling scenarios result in a declining reef trajectory by the end of the simulated timeframe. This suggests that, in the absence of drastic reductions of gas emissions, solar radiation management alone might be insufficient to ensure long-term reef persistence in the Cairns region.

(A) RCP 2.6, low adaptation potential



(B) RCP 2.6, high adaptation potential

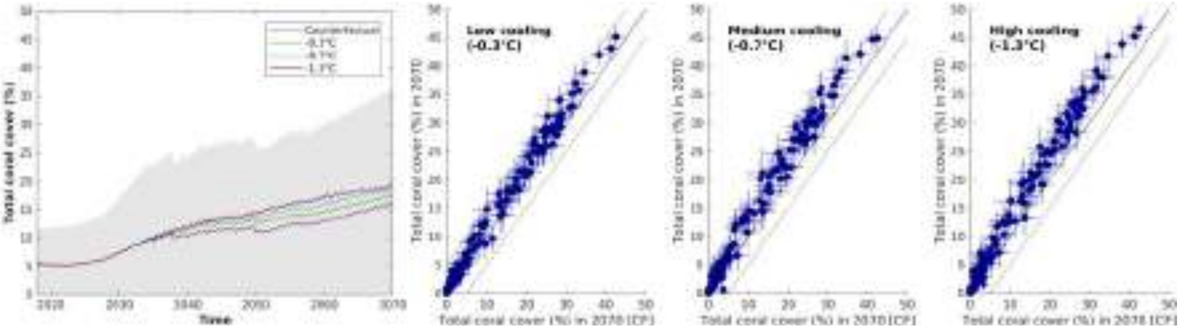
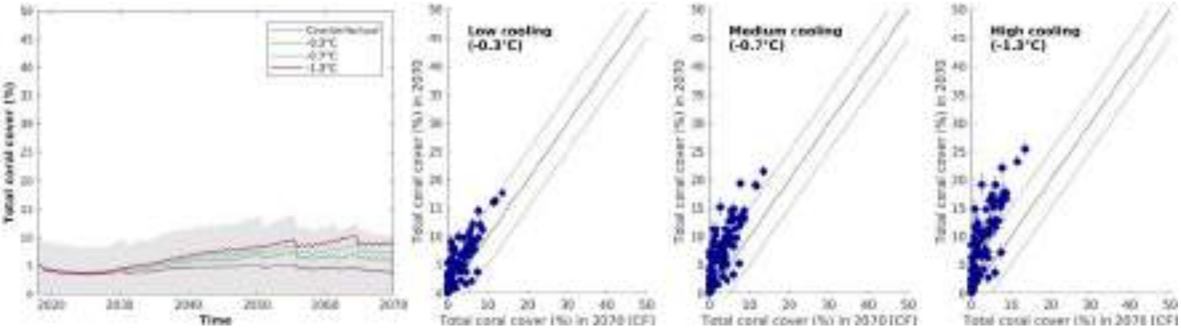


Fig. 56: Long-term ecological benefits of solar radiation management under low carbon emission (RCP 2.6) scenario.

(A) RCP 8.5, low adaptation potential



(B) RCP 8.5, high adaptation potential

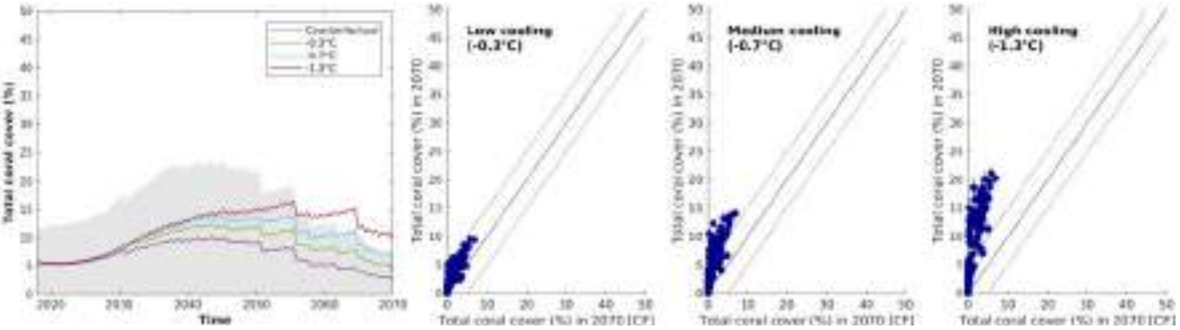


Fig.57: Long-term ecological benefits of solar radiation management brightening under low carbon emission (RCP 8.5) scenario

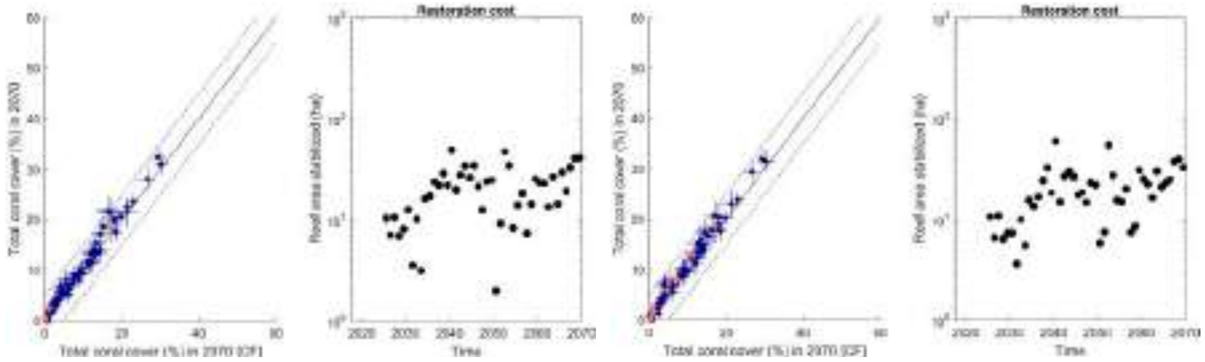
B2.3.5 Rubble stabilisation

Artificial stabilisation of loose rubble on the reef was modelled by setting rubble cover to 0 percent on reefs targeted for restoration, which results essentially in resetting coral juvenile survival to the default value (0.9 over six months). Simulations (2018–2070) were performed whereby 10 to 20 reefs are restored yearly from 2025 onward. Here again, the best donor reefs were used as priority reefs for intervention, provided that current rubble cover is above five percent in any given year. As for coral deployment, restoration moves to another reef down the priority list if rubble cover is below this threshold. Restoration cost is calculated every year as the total area of stabilised substratum across the Cairns region.

Under RCP 2.6 and low adaptation potential, rubble stabilisation has no detectable effect on the regional coral cover (Fig. 58). Being generated from coral loss after disturbance, rubble cover remains globally low (max. ~10 percent) due to the low levels of coral cover (max. ~10 percent) maintained on all reefs over the course of simulation (see Fig. 47A). Hence, the stabilisation of small rubble beds (i.e. five-10 percent rubble cover) has a limited impact on the survival of juveniles which is close to the optimum value. Once a reef is restored and rubble cover set to 0 percent, it takes a long time before rubble exceeds five percent again because disturbances can only generate a small amount of rubble at a time, and most of it is rapidly stabilised by natural processes of cementation. As a result, reefs selected for intervention largely extend the priority list with many substitute reefs being visited at multiple occasions, so that restoring 10 or 20 reefs produces similar ecological outcomes and restoration costs.

Inversely, the impact of artificial rubble stabilisation appears significant under RCP 2.6 and high adaptation potential (Fig. 58B). This is essentially because corals achieve greater coverage (see Fig.47B) and so does rubble generated by acute disturbances. A slightly greater production of rubble (max. ~15 percent) is enough to affect coral demographics in such a way that the benefits of forced rubble stabilisation become substantial. While this highlights that loose rubble has a greater impact where corals are abundant, it merely reveals the magnitude of the negative feedback that impede coral recovery. One important implication is that healthy reefs today are likely to benefit the most from rubble stabilisation post-disturbance. It is certainly more cost-efficient to focus intervention on reefs where rubble is abundant rather than dispersing the restoration effort. Moreover, it can be anticipated that much greater regional benefits might be achieved with a strategy that optimises the sequence by which reefs are selected for rubble stabilisation. In particular, the threshold value of rubble cover used to trigger intervention is likely to have a disproportionate effect on the benefits measured at the scale of the region. Importantly, the impacts of rubble stabilisation can be overlooked in cost-benefit analyses based on pessimistic reef state projections, i.e. the ‘rubble problem’ is contingent to the amount of corals available prior to disturbance.

(A) RCP 2.6, low adaptation potential



10 restored reefs

20 restored reefs

(B) RCP 2.6, high adaptation potential

10 restored reefs 20 restored reefs

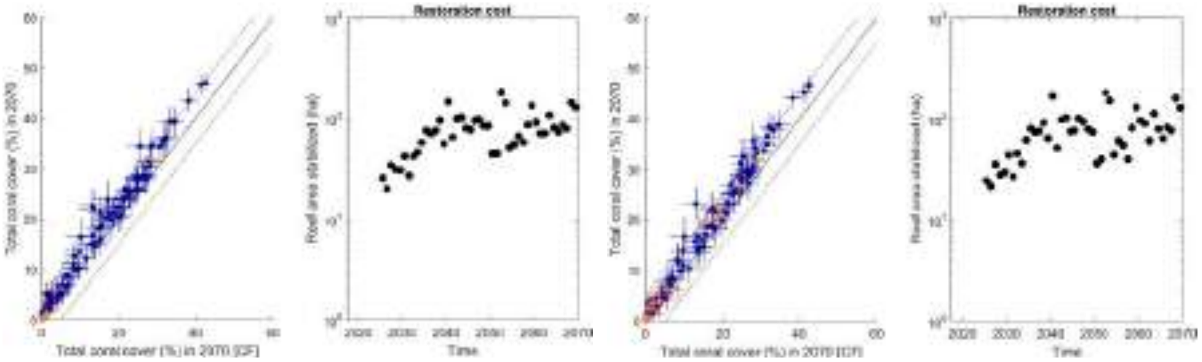
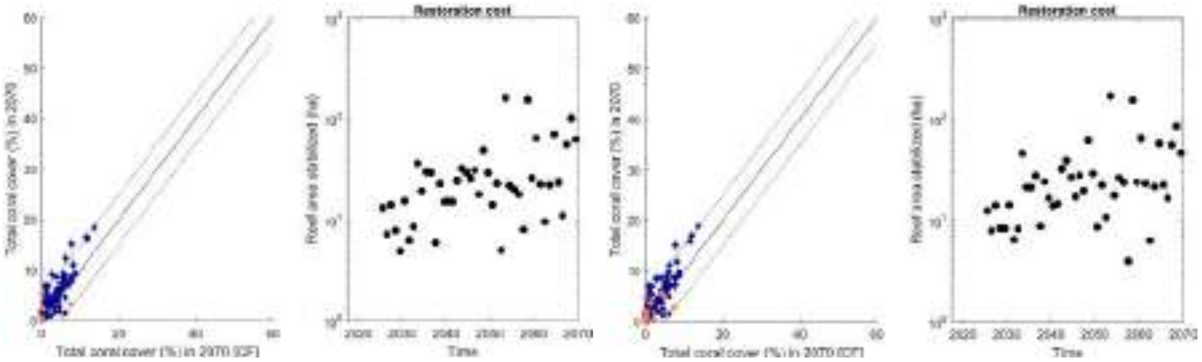


Fig.58: Long-term ecological benefits of rubble stabilisation under low carbon emissions (RCP 2.6). Orange dots indicate priority reefs. Error bars indicate SD of reef coral cover over 40 replicate runs.

Under RCP 8.5, rubble stabilisation has no noticeable effect on coral cover for any scenario of adaptation and deployment strategy (Fig.59). Similar to the RCP 2.6 scenario of low adaptation potential, reefs maintain levels of coral cover that are too low to create amounts of rubble after disturbance that can significantly impede juvenile survival.

(A) RCP 8.5, low adaptation potential

10 restored reefs 20 restored reefs



(B) RCP 8.5, high adaptation potential

10 restored reefs 20 restored reefs

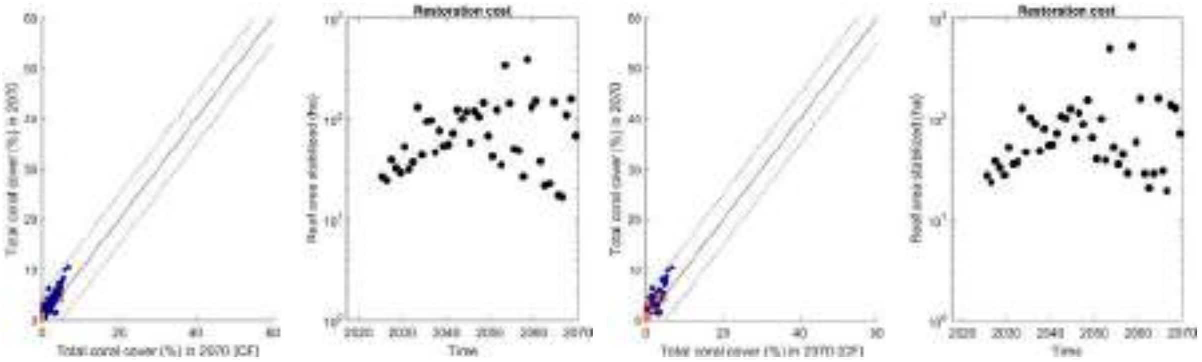


Fig.59: Long-term ecological benefits of rubble stabilisation under high carbon emissions (RCP 8.5).

Appendix B2 References

Anthony, K., M. O. Hoogenboom, J. A. Maynard, A. G. Grottoli, and R. Middlebrook. 2009. Energetics approach to predicting mortality risk from environmental stress: a case study of coral bleaching. Functional ecology 23:539–550.

Baird, A., and P. Marshall. 2002. Mortality, growth and reproduction in scleractinian corals following bleaching on the Great Barrier Reef. Marine Ecology Progress Series 237:133–141.

Baird, M. E., M. P. Adams, J. Andrewartha, N. Cherukuru, M. Gustafsson, S. Hadley, M. Herzfeld, E. Jones, N. Margvelashvili, M. Mongin, and others. 2017. CSIRO environmental modelling suite: scientific description of the optical, carbon chemistry and biogeochemical models (BGC1p0).

Baria, M. V. B., R. D. Villanueva, and J. R. Guest. 2012. Spawning of Three-Year-Old Acropora Millepora Corals Reared from Larvae in Northwestern Philippines. Bulletin of Marine Science 88:61–62.

Berkelmans, R. 2002. Time-integrated thermal bleaching thresholds of reefs and their variation on the Great Barrier Reef. Marine ecology progress series 229:73–82.

Biggs, B. C. 2013. Harnessing natural recovery processes to improve restoration outcomes: an experimental assessment of sponge-mediated coral reef restoration. PloS one 8:e64945.

Bozec, Y.-M., L. Yakob, S. Bejarano and P. J. Mumby. 2013. Reciprocal facilitation and non-linearity maintain habitat engineering on coral reefs. Oikos 122: 428-440.

Bozec, Y.-M., S. O’Farrell, J. H. Bruggemann, B. E. Luckhurst, and P. J. Mumby. 2016. Tradeoffs between fisheries harvest and the resilience of coral reefs. Proceedings of the National Academy of Sciences of the United States of America 113:4536–4541.

Bozec, Y.-M., L. Alvarez-Filip, and P. J. Mumby. 2015. The dynamics of architectural complexity on coral reefs under climate change. Global Change Biology 21:223–235.

Bozec, Y.-M., C. Doropoulos, G. Roff, and P. J. Mumby. 2019. Transient Grazing and the Dynamics of an Unanticipated Coral–Algal Phase Shift. Ecosystems 22:296-311..

Casey, K., E. Selig, D. Zhang, K. Saha, A. Krishnan, and E. McMichael. 2015. The Coral Reef Temperature Anomaly Database (CoRTAD) Version 5—Global, 4 km sea surface temperature and related thermal stress metrics for 1982–2012. NOAA National Centers for Environmental Information. Dataset. doi 10:V5CZ3545.

Chen, Y., S. Minchin, S. Seaton, K. Joehnk, B. Robson, Q. Bai, F. Chan, D. Marinova, and R. Anderssen. 2011. eReefs–a new perspective on the Great Barrier Reef. Pages 12–16 19th International Congress on Modelling and Simulation, Perth, Australia.

Condie, S. A., M. Hepburn, and J. Mansbridge. 2012. Modelling and visualisation of connectivity on the Great Barrier Reef. Pages 9–13 Proceedings of the 12th International Coral Reef Symposium.

Connell, J. H. 1997. Disturbance and recovery of coral assemblages. Coral reefs 16:S101–S113.

Connolly, S. R., and A. H. Baird. 2010. Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. Ecology 91:3572–3583.

Dollar, S., and G. Tribble. 1993. Recurrent storm disturbance and recovery: a long-term study of coral communities in Hawaii. Coral Reefs 12:223–233.

Doropoulos, C., G. Roff, Y.-M. Bozec, M. Zupan, J. Werminghausen, and P. J. Mumby. 2016. Characterizing the ecological trade-offs throughout the early ontogeny of coral recruitment. Ecological Monographs 86:20–44.

Doropoulos, C., S. Ward, G. Roff, M. González-Rivero, and P. J. Mumby. 2015. Linking demographic processes of juvenile corals to benthic recovery trajectories in two common reef habitats. PLoS One 10:e0128535.

Edmunds, P. J. 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. Oecologia 146:350–364.

Edwards, H. J., I. A. Elliott, C. M. Eakin, A. Irikawa, J. S. Madin, M. McField, J. A. Morgan, R. van Woesik, and P. J. Mumby. 2011. How much time can herbivore protection buy for coral reefs under realistic regimes of hurricanes and coral bleaching? Global Change Biology 17:2033–2048.

Emslie, M., A. Cheal, H. Sweatman, and S. Delean. 2008. Recovery from disturbance of coral and reef fish communities on the Great Barrier Reef, Australia. Marine Ecology Progress Series 371:177–190.

Fabricius, K., K. Okaji, and G. De'Ath. 2010. Three lines of evidence to link outbreaks of the crown-of-thorns seastarcrown-of-thorns starfish Acanthaster planci to the release of larval food limitation. Coral Reefs 29:593–605.

Fox, H. E., J. S. Pet, R. Dahuri, and R. L. Caldwell. 2003. Recovery in rubble fields: long-term impacts of blast fishing. Marine Pollution Bulletin 46:1024–1031.

Garde, L., C. Spillman, S. Heron, and R. Beeden. 2014. Reef Temp Next Generation: A new operational system for monitoring reef thermal stress. Journal of Operational Oceanography 7:21–33.

Great Barrier Reef Marine Park Authority. 2007. Great Barrier Reef (GBRReef) Features (Reef boundaries, QLD Mainland, Islands, Cays, Rocks and Dry Reefs) (GBRMPA). eAtlas.

Hall, V., and T. Hughes. 1996. Reproductive strategies of modular organisms: comparative studies of reef-building corals. Ecology 77:950–963.

Herzfeld, M., J. Andrewartha, M. Baird, R. Brinkman, M. Furnas, P. Gillibrand, M. Hemer, K. Joehnk, E. Jones, D. McKinnon, and others. 2016. eReefs Marine Modelling: Final Report, Jan. 2016, CSIRO, Hobart, 497 pp.

Hock, K., N. H. Wolff, S. A. Condie, K. Anthony, and P. J. Mumby. 2014. Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. Journal of applied ecology 51:1188–1196.

Hock, K., N. H. Wolff, J. C. Ortiz, S. A. Condie, K. R. Anthony, P. G. Blackwell, and P. J. Mumby. 2017. Connectivity and systemic resilience of the Great Barrier Reef. PLoS biology 15:e2003355.

Hughes, T. P., J. T. Kerry, M. Álvarez-Noriega, J. G. Álvarez-Romero, K. D. Anderson, A. H. Baird, R. C. Babcock, M. Beger, D. R. Bellwood, R. Berkelmans, and others. 2017. Global warming and recurrent mass bleaching of corals. Nature 543:373.

Hughes, T. P., J. T. Kerry, A. H. Baird, S. R. Connolly, A. Dietzel, C. M. Eakin, S. F. Heron, A. S. Hoey, M. O. Hoogenboom, G. Liu, and others. 2018. Global warming transforms coral reef assemblages. Nature 556:492.

Humanes, A., A. Fink, B. L. Willis, K. E. Fabricius, D. de Beer, and A. P. Negri. 2017a. Effects of suspended sediments and nutrient enrichment on juvenile corals. Marine pollution bulletin 125:166–175.

Humanes, A., G. F. Ricardo, B. L. Willis, K. E. Fabricius, and A. P. Negri. 2017b. Cumulative effects of suspended sediments, organic nutrients and temperature stress on early life history stages of the coral Acropora tenuis. Scientific reports 7:44101.

Jones, R., G. Ricardo, and A. Negri. 2015. Effects of sediments on the reproductive cycle of corals. Marine Pollution Bulletin 100:13–33.

Keesing, J., and J. Lucas. 1992. Field measurement of feeding and movement rates of the crown-of-thorns starfish Acanthaster planci (L.). Journal of experimental marine biology and ecology 156:89–104.

Keim, B. D., R. A. Muller, and G. W. Stone. 2007. Spatiotemporal patterns and return periods of tropical storm and hurricane strikes from Texas to Maine. Journal of climate 20:3498–3509.

Kettle, B., and J. Lucas. 1987. Biometric relationships between organ indices, fecundity, oxygen consumption and body size in Acanthaster planci (L.)(Echinodermata; Asteroidea). Bulletin of Marine Science 41:541–551.

MacNeil, M. A., C. Mellin, M. S. Pratchett, J. Hoey, K. R. Anthony, A. J. Cheal, I. Miller, H. Sweatman, Z. L. Cowan, S. Taylor, and others. 2016. Joint estimation of crown of thorns (Acanthaster planci) densities on the Great Barrier Reef. PeerJ 4:e2310.

Marshall, A. T., and P. Clode. 2004. Calcification rate and the effect of temperature in a zooxanthellate and an azooxanthellate scleractinian reef coral. Coral reefs 23:218–224.

Matz, M. V., E. A. Treml, G. V. Aglyamova, and L. K. Bay. 2018. Potential and limits for rapid genetic adaptation to warming in a Great Barrier Reef coral. PLoS genetics 14:e1007220.

Moran, P., and G. De'Ath. 1992. Estimates of the abundance of the crown-of-throns starfish Acanthaster planci in outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef. Marine Biology 113:509–515.

Mumby P. J. 1999 Bleaching and hurricane disturbances to populations of coral recruits in Belize. Marine Ecology Progress Series 190, 27–35.

Mumby, P. J. 2006. The impact of exploiting grazers (Scaridae) on the dynamics of Caribbean coral reefs. Ecological Applications 16:747-769.

Mumby, P. J., A. Hastings, and H. J. Edwards. 2007. Thresholds and the resilience of Caribbean coral reefs. Nature 450:98–101.

Mumby, P. J., N. H. Wolff, Y.-M. Bozec, I. Chollett, and P. Halloran. 2014. Operationalizing the resilience of coral reefs in an era of climate change. Conservation Letters 7:176–187.

Ortiz, J. C., Y.-M. Bozec, N. H. Wolff, C. Doropoulos, and P. J. Mumby. 2014. Global disparity in the ecological benefits of reducing carbon emissions for coral reefs. Nature Climate Change 4:1090.

Pratchett, M. S., C. F. Caballes, J. A. Rivera-Posada, and H. P. Sweatman. 2014. Limits to understanding and managing outbreaks of crown-of-thorns starfish (Acanthaster spp.). Oceanography and Marine Biology: An Annual Review 52:133–200.

Puotinen, M., J. A. Maynard, R. Beeden, B. Radford, and G. J. Williams. 2016. A robust operational model for predicting where tropical cyclone waves damage coral reefs. Scientific reports 6:26009.

Rasser, M., and B. Riegl. 2002. Holocene coral reef rubble and its binding agents. Coral Reefs 21:57–72.

Richmond, R. H. 1997. Reproduction and recruitment in corals: critical links in the persistence of reefs. Life and death of coral reefs. Chapman & Hall, New York:175–197.

Robson, B. J., M. Baird, and K. Wild-Allen. 2013. A physiological model for the marine cyanobacteria, Trichodesmium. Pages 978–0 MODSIM2013, 20th International Congress on Modelling and Simulation. Modelling and Simulation Society of Australia and New Zealand, ISBN.

Roelfsema, C., Kovacs, E., Roos, P., Terzano, D., Lyons, M., & Phinn, S. (2018). Use of a semi-automated object-based analysis to map benthic composition, Heron Reef, Southern Great Barrier Reef. Remote Sensing Letters, 9(4), 324-333.

Rogers, A., J. L. Blanchard, S. P. Newman, C. S. Dryden, and P. J. Mumby. 2018. High refuge availability on coral reefs increases the vulnerability of reef-associated predators to overexploitation. Ecology 99:450–463.

Sano, M., M. Shimizu, and Y. Nose. 1987. Long-term effects of destruction of hermatypic corals by Acanthaster planci infestation on reef fish communities at Iriomote Island, Japan. Marine Ecology Progress Series:191–199.

Trapon, M. L., M. S. Pratchett, and A. S. Hoey. 2013. Spatial variation in abundance, size and orientation of juvenile corals related to the biomass of parrotfishes on the Great Barrier Reef, Australia. PloS one 8:e57788.

Vermeij, M. J., and S. A. Sandin. 2008. Density-dependent settlement and mortality structure the earliest life phases of a coral population. Ecology 89:1994–2004.

Viehman, T. S., J. L. Hench, S. P. Griffin, A. Malhotra, K. Egan, and P. N. Halpin. 2018. Understanding differential patterns in coral reef recovery: chronic hydrodynamic disturbance as a limiting mechanism for coral colonization. Marine Ecology Progress Series 605:135–150.

Wallace, C. 1999. Staghorn corals of the world: a revision of the genus Acropora. CSIRO publishing.

Wolff, N. H., S. D. Donner, L. Cao, R. Iglesias-Prieto, P. F. Sale, and P. J. Mumby. 2015. Global inequities between polluters and the polluted: climate change impacts on coral reefs. Global Change Biology 21:3982–3994.

Wolff, N. H., P. J. Mumby, M. Devlin, and K. Anthony. 2018. Vulnerability of the Great Barrier Reef to climate change and local pressures. Global change biology.

Wolff, N. H., A. Wong, R. Vitolo, K. Stolberg, K. R. Anthony, and P. J. Mumby. 2016. Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. Coral Reefs 35:613–623.

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