Australian Government
Great Barrier Reef
Marine Park Authority

Queensland
Government

Supplementary Report to the Final Report of the Coral Reef Expert Group:

S7. Coral reef models as assessment and reporting tools for the Reef 2050 Integrated Monitoring and Reporting Program – a review

Bozec, Y.-M., Mumby, P. J.

University of Queensland

The Great Barrier Reef Marine Park Authority acknowledges the continuing sea country management and custodianship of the Great Barrier Reef by Aboriginal and Torres Strait Islander Traditional Owners whose rich cultures, heritage values, enduring connections and shared efforts protect the Reef for future generations.

Published by the Great Barrier Reef Marine Park Authority

ISBN 9780648721413

A catalogue record for this publication is available from the National Library of Australia

This publication should be cited as:

Bozec, Y. M., and Mumby, P. J. 2019, *Supplementary Report to the Final Report of the Coral Reef Expert Group: S7. Coral reef models as assessment and reporting tools for the Reef 2050 Integrated Monitoring and Reporting Program – a review*, Great Barrier Reef Marine Park Authority, Townsville.

Front cover image: Coral © Commonwealth of Australia (GBRMPA), photographer: Chris Jones.

DISCLAIMER

Australian Government
Great Barrier Reef
Marine Park Authority

Great Barrier Reef Marine Park Authority
280 Flinders Street Townsville | PO Box 1379 Townsville QLD 4810
Phone: (07) 4750 0700
Fax: 07 4772 6093
Email: info@gbrmpa.gov.au
www.gbrmpa.gov.au

Contents

Executive Summary

The objective of this report is to review the existing models of temporal/spatial dynamics of coral communities available for the Great Barrier Reef (the Reef), with the specific aim at evaluating their strengths and weaknesses for the assessment and reporting of coral reef health within the Reef 2050 Integrated Monitoring and Reporting Program (RIMReP). Focusing on peer-reviewed articles available by 28 February 2018, we found that a variety of modeling approaches exists yet with different scope, level of complexity, and ability to represent the various processes driving the dynamics of coral populations. Tools available to model Reef coral population dynamics also vary in their capacity to capture the spatial heterogeneity of coral populations and their environment, the variability of disturbance impacts and the uncertainty around current reef state and possible future trajectory. The various characteristics and properties exhibited by coral reef models means they have different capacities to complement reef monitoring and assessment on the Reef. This review provides guidance for integrating a modeling component to RIMReP by identifying the modeling approaches that offer the strongest support to reef monitoring and management.

The report is organised as follows: In section 1, we list the potential benefits of ecological models for monitoring programs and explain how models can complement monitoring data and support the assessment of reef status and trends across the Reef. Section 2 provides an overview of the general characteristics and properties of ecological models, with the aim of facilitating the technical comparison of available coral reef models. In section 3, we summarise what we think are the key processes that influence the dynamics of coral populations. This provides a mechanistic framework allowing a comparison of models based on their ecological realism, i.e. their ability to reproduce changes in coral populations from the compounded action of individual demographic mechanisms. Section 4 provides an overview of the candidate coral models for the Reef, with their summary characteristics (model type, state variables, time steps), the ecological processes embedded, their parametrisation and model's ability to capture the spatial dynamics of corals in a heterogeneous environment. For each model we highlight their strengths and weaknesses in complementing monitoring data to inform about status and trends across the Reef. Finally, we synthesise in section 5 the best candidate models, highlight their ability to inform management priorities for the Reef and make a number of recommendations for a successful integration into RIMReP.

1.0 Potential benefits of a modeling framework for monitoring

Ecological models are predictive tools that can offer great support to monitoring and assessment programs. Model predictions can be viewed as expectations regarding the prevalence of specific demographic processes, ecological interactions and/or disturbances in a particular environment. Therefore, confronting model expectations with real observations can provide important insights into the underlying processes generating patterns. Model predictions also offer a first estimation of ecosystem health in systems that are yet to be surveyed. Moreover, by integrating processes, models can be used to make short-term predictions for the fate of an ecosystem and thereby add value to monitoring or snapshot survey data. The most sophisticated models, i.e. those integrating the multiple mechanisms that drive the dynamics of individual organisms in a spatial context, are arguably the most predictive and can also be used to predict emergent properties of reefs such as their functioning for coastal protection and fisheries. In the following we consider the benefits of using models as **diagnostic**, **prognostic** and **exploratory tools** in support of monitoring and assessment. Model capacities and benefits are summarised in **Table 1** below.

Table 1. Examples of model capacities and their potential use for assessment and monitoring

Model capacities	Operational benefits for monitoring
Diagnostic	
- predict current state	Confirm or challenge current understanding about reefs when model predictions do not align with observations Fill monitoring gaps with model-based expectations Guide monitoring effort (*include new sites, intensify sampling where model predictions conflict with observations)*
- indicate recent change in state	Contextualise monitoring data (*provide greater accuracy to field assessment, inform about possible trends when uncertain)*
- identify the nature and cause of change	Explain recent dynamics with ecological processes Identify source of stress Guide management intervention (*mitigation & restoration*)
- anticipate further change	Indicate ongoing changes (*detections of trends not yet confirmed by monitoring data because of large uncertainty*) Guide monitoring effort (*priorisation*) Guide management intervention (*mitigation & restoration*)
Prognostic	
- predict future trajectory	Set management objectives (*targets*) Measure progress towards achievement of targets
Exploratory	
- simulate management interventions	Evaluate the feasibility of a specific intervention Quantify benefits and tradeoffs of alternative options Incentive for action (*decision*) and funding (*communication*)

The intent of this section of the report is to describe the information needs that inform the design requirements for monitoring the specific values considered by the thematic expert group.

1.1 Models as diagnostic tools

Ecological models can be efficient diagnostic tools that help interpret reef monitoring data and prioritise monitoring effort. Model expectations about the current state and past behavior of a reef environment might align or not with field observations, yet both situations are informative for the monitored system. An agreement between model and data will provide greater accuracy to current assessments (i.e. those affected by high levels of uncertainty) and will increase confidence in the causes of current Reef health. Model hindcast of recent ecosystem changes can help contextualise monitoring data by informing about possible trends that are not well captured by the surveys due to strong variability in the measured metrics and/or observation errors.

Discrepancies between model predictions and field observations can also be informative. First, they allow questioning the data and may highlight imprecise or erroneous observations that would require additional sampling (for example where a reported increase in coral cover would exceed even the wildest expectations based on known rates of population growth). Second, large discrepancies between models and data may reveal deficient knowledge or erroneous assumptions about Reef dynamics and exposure to disturbances. For example, extensive cyclone impacts might have been anticipated on a particular Reef site due to its proximity to the cyclone track, while in reality this location escaped damages owing to protection provided by nearby reefs. Inversely, a reef that fares better than expected based on model predictions would suggest that further exploration of resistance or recovery properties warrant further study.

Complex models that integrate the component mechanisms of coral demographics (e.g. recruitment, colony growth and mortality) can link ecological trends to a particular process or external stress. Such models offer valuable insights into monitoring because they are more likely to anticipate future trends.

Finally, ecological models can inform about possible status and trends of reefs that are not covered by a monitoring program. This is particularly important considering the size of the Great Barrier Reef (the Reef) which precludes exhaustive sampling. Such predictions, while not confirmed by observations, provide useful information to prioritise sampling and some management actions.

1.3 Models as prognostic tools

Of particular interest for monitoring and management is the prediction of coral reef state at different time horizons for what is thought to be a realistic scenario of acute disturbance a (e.g. coral bleaching, cyclones, population outbreaks). Predictive scenarios allow envisioning the long-term sustainability of reef health and thus help defining management objectives, strategies and Outlook reporting. They can also serve as a reference for evaluating progress towards targets and objectives.

1.3 Models as exploratory tools

Models can also be used to compare different scenarios of management intervention by evaluating their benefits and costs relative to predictions of Reef health at various time horizons. For example, a model that integrates the impacts of suspended sediments or turbidity on coral populations can be used to draw scenarios of water quality improvements and evaluate their relative benefits on various reef metrics (e.g. coral cover, density of juvenile corals, algal cover). Predictions of the impacts of different tactical interventions must come with estimates of uncertainty in model outputs (including the benefits and costs) so that managers are provided with levels of risk to help select the most efficient options.

2.0 General characteristics of ecological models

We define here some general characteristics and properties of ecological models that inform the choice for a particular application. Here we define the terminology used in **Appendix 1 summary table** which compares the candidate models.

2.1 Theoretical vs. applied

We refer here to the pragmatic-theoretic axis (DeAngelis and Yurek 2017) to discriminate among ecological models that address applied or theoretical questions. Applied (pragmatic) models usually perform ecological simulations to explore system behavior in response to different scenarios; such models are essentially predictive and are often developed to inform and support management decisions. Simulation models typically fall in this category. They tend to be more complex, require more parameters and are often spatially-explicit. On the other hand, theoretical models are usually developed to analyse a particular phenomenon, e.g. the direction and magnitude of an ecological response to a specific disturbance. They often rely on an extreme simplification of ecological processes in order to focus on the dynamics of interest. Analytical models fall within this category.

2.2 Analytical vs. Computational

Analytical models are equation-based models that do not involve statistics or probabilities in their formulation. They are typically based on a system of ordinary differential/difference equations that can be solved mathematically using numerical integration. By contrast, computational models require the development of a program that describes the structure and executes the behavior of the modeled system. The model is typically analysed through the simulation of system behavior, and for this reason computational models are often conflated with simulation models. We prefer the term computational as analytical models can also be used to simulate the dynamics of the modeled system. Here we refer to simulation as the step-by-step execution of a model and restrict its use to the temporal reproduction of the behavior of a system (i.e. simulation of temporal dynamics).

2.3 Predictive vs. descriptive

Here we consider as descriptive a model that is mostly used to explore the behavior or the dynamic properties of a system. A descriptive model does not necessarily require the support of empirical data to be informative; model variables and parameters can have abstract or arbitrary values or can be defined as relative indices without affecting the dynamics of the modeled system. By opposition a predictive model is built on a robust and realistic parameterisation (e.g. actual rates of coral recruitment) and offers more realism to the modeled quantities (e.g. a number of coral colonies over a given reef surface). Such model can predict future outcomes but its predictive capacity must be supported by rigorous testing and validation.

2.4 Individual-based vs population models

Individual-based models are computational models that simulate populations or system of populations as discrete agents or individuals (DeAngelis and Grimm 2014). Each modeled individual is characterised by a set of state variables or attributes whose value may vary over time independently from the other individuals. Such models allow for the emergence of population-level behavior from the evolution of individuals and their interactions with each other and their environment. They often form the most sophisticated models as they allow for the integration of individual-level mechanisms and behaviors (mechanistic models), including movements.

We refer to population models, those demographic models where populations are generally represented by a single aggregative variable (e.g. abundance, biomass) so that individual-level information is lost. Note that some population models disaggregate their state variable into subpopulations determined by their age (e.g. adult vs juvenile) or size.

2.5 Budget models

These models describe the flow of energy or matter (food) through the various components of a system. Their focus is the identification of important trophic pathways within a system and how each component utilises their trophic resources for maintenance, growth and reproduction.

2.6 Spatial models

A model has a spatial structure which includes (but is not restricted to) the definition of spatial units (patches) of populations characterised by different parameter values, the integration of spatial processes such as population connectivity through larval dispersal and/or spatial patterns of environmental forcing. With this definition, a spatial model does not necessarily include interacting populations so that the behavior of spatially-located individual, population or community is affected by the behavior of its neighborhood population.

A model is spatially-realistic when its spatial structure reflects the arrangement of patches observed in a real system, and when parameter values are truly representative of the heterogeneity in processes or patterns observed across space. Spatial resolution of models includes the grain (minimum spatial unit of the model) and extent (size of the modeled world).

2.7 Deterministic vs. stochastic

In deterministic models, any model output is fully determined by the parameter values and the initial conditions. This means that the execution of the model will always produce the same output with the same parameter values. For this reason, a model that runs with randomly-generated parameter values (i.e. with values sampled from a predefined interval) is deterministic if those parameters are kept constant over a simulation.

Stochastic models possess some inherent randomness, so that uncertainty in parameters is built internally at each time step. As a result, the same set of parameter values always leads to a different model outcome.

The way a model handles uncertainty (i.e. internally or externally through parameter variability) has important implications in the definition of envelops of predictions.

3.0 Key ecological processes and their integration in coral models

The growth or maintenance of populations of hard corals at a given reef site is generally measured by the area of substratum that is colonised by individual coral colonies. Estimating percentage hard coral cover is a very convenient way to measure the size of coral populations, partly because this involves fast and cost-effective sampling, but also because hard coral cover is an indicator of reef health. Thus, most (if not all) programs of reef monitoring rely on the assessment of coral cover. Perhaps not surprisingly, many models of coral dynamics use coral cover as the modeled variable.

Particularly important for monitoring is the detection of changes in coral cover, because they indicate the incidence of substantial coral mortality (decreasing cover) or, inversely, that coral populations are recovering after disturbance (increasing cover). For this reason, simple models of population growth have been used to model changes in coral cover. The simplest model assumes that the rate of population growth is constant, but this implies that coral populations grow linearly and are not limited by available space. A more realistic assumption is that population (as coral cover) growth rate decreases with increasing coral cover due to density-dependent mechanisms (e.g. increased competition in a saturated space). Typical models of nonlinear growth use a sigmoidal curve to describe population changes, such as the simple **logistic** (Verhulst) and the Gompertz functions.

Irrespective of the choice of the growth function, simple models of population growth make the implicit assumption that the growth function captures the net outcome of concurrent mechanisms that affect the number and size of coral colonies. However, a number of demographic processes and ecological interactions drive the dynamics of corals (**Figure 1**) and, considering the variety of reef environments in the Reef, the intensity of these mechanisms is likely to vary from reef to reef. As a result, a simple dynamic model of coral cover using a single growth function is **unlikely to fit coral population dynamics everywhere**.

On the other hand, models that account for the complexity of coral demographics and the variability of their rates provide a more reliable representation of coral populations along environmental gradients. Parameterisation of individual mechanisms can be supported by *in situ* observations (e.g. assessing skeletal growth of juvenile corals along a temperature gradient), or experimental data (e.g. measuring the dose-response relationship between temperature and skeletal growth of juveniles in a controlled environment). Note that simpler models are not exempt of sampling effort, as a reliable parameterisation requires multiple observations of coral cover in diverse environments (e.g. representative population growth rates along a temperature gradient).

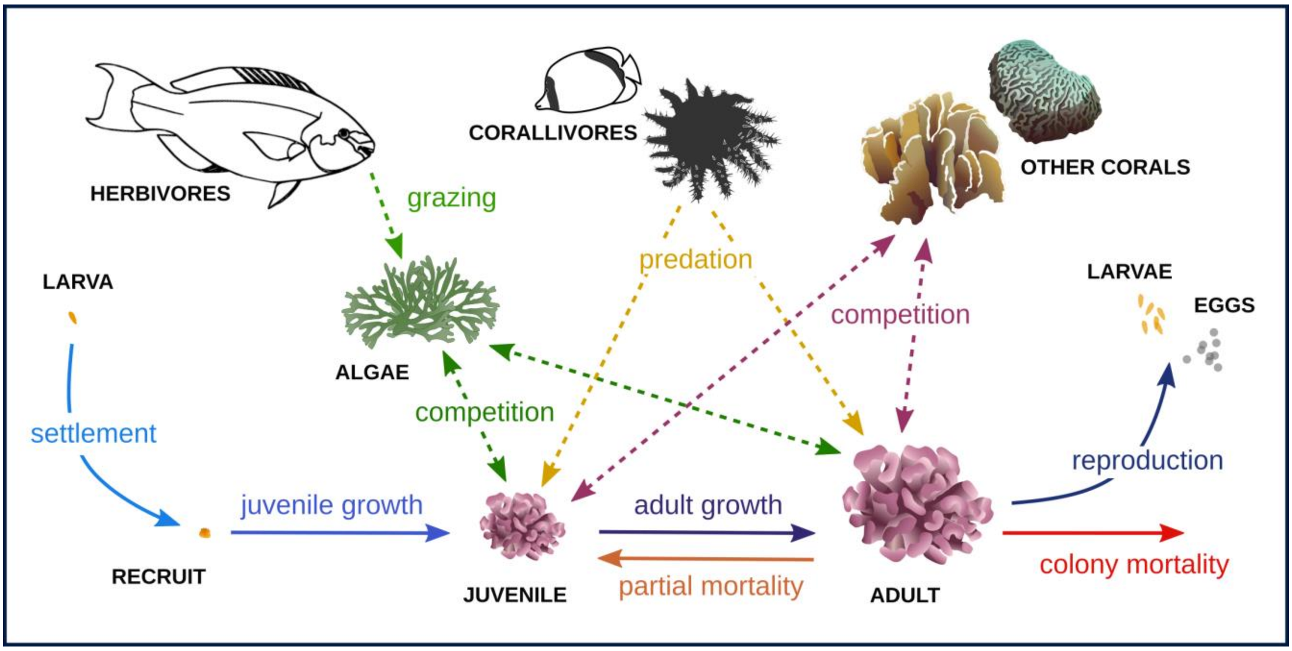
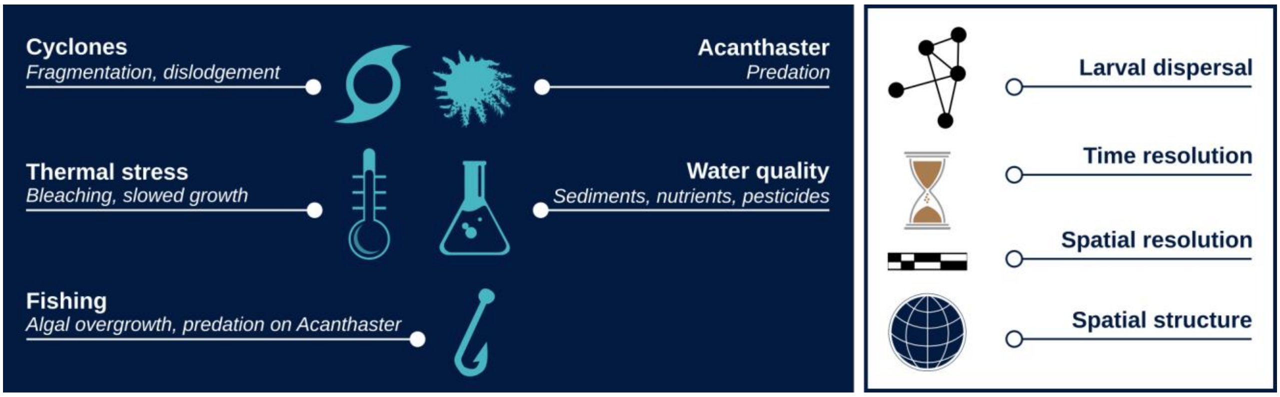


Figure 1. Conceptual model of some key processes (solid arrows) and interactions (dashed arrows) driving coral population dynamics on the Great Barrier Reef. *Source of symbols: IAN image library and YM Bozec.*

Modeling the core mechanisms of coral demographics also allows for capturing the chronic effects of disturbances on coral populations. Acute disturbances, such as cyclones, bleaching, or population outbreaks of the crown-of-thorns starfish, can be easily modeled by a sudden loss of coral cover reflective of an acute mortality event. Some disturbances, however, do not kill corals suddenly but continuously, at rates that might only be perceptible in the long term. Other processes than mortality (e.g. settlement rate, skeletal growth) and even interactions (e.g. with algae) can be affected by chronic stress but their consequences on coral cover are difficult to predict and challenge the parameterisation of simple dynamic models. However, with the explicit modeling of demographic mechanisms under stress, chronic impacts of disturbance on coral cover can emerge from the simulation of the modeled processes.

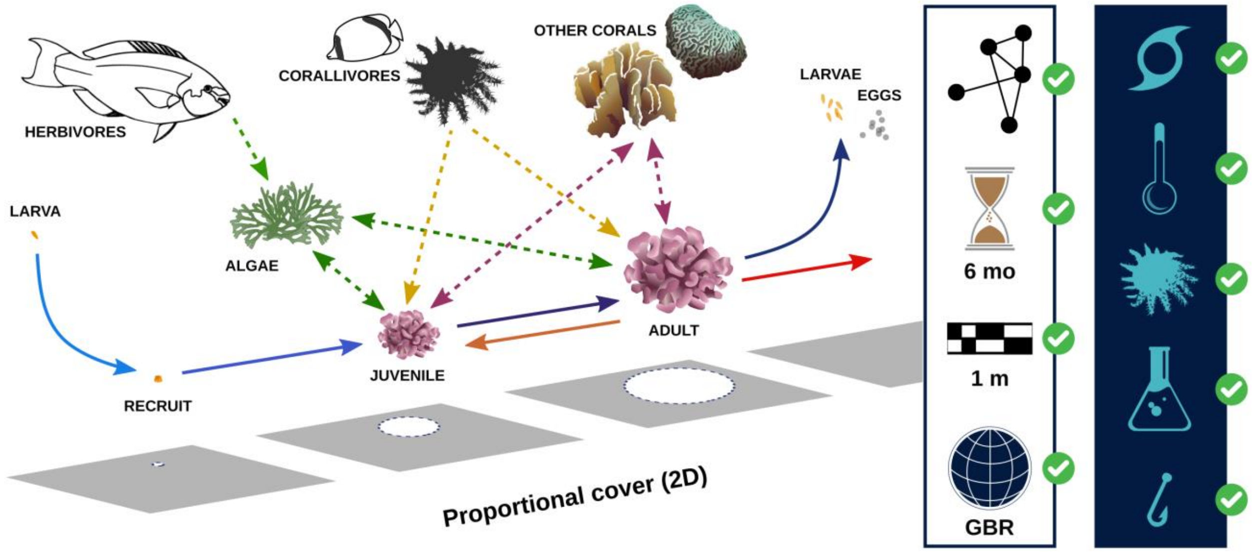
4.0 Candidate coral reef models for RIMReP

We found 13 coral-based models applied to the Reef and published as peer-reviewed articles (by 28 February 2018). We note that additional models, such as CORSET (Melbourne-Thomas et al. 2011) and ATLANTIS (Fulton et al. 2011, Weijerman et al. 2015) might be considered of interest if a specific parametrisation becomes available for the Reef. The models are listed below in decreasing order of complexity and summarised using the schematic of **Figure 1** complemented with the following symbols. Model characteristics are summarised in **Appendix 1.**



4.1 Reefmod

Mumby et al. 2007, 2014; Edwards et al. 2011; Ortiz et al. 2014; Bozec et al. 2015, 2016



Description: Reefmod is a spatially-explicit model of coral population dynamics that was 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 parametrised to simulate coral reef dynamics on the Reef (Ortiz et al. 2014). The model is individual-based and simulates the fate of coral colonies across a 20m × 20m grid of 1m × 1m cells. Model agents include coral colonies of 6 morphological groups and individual patches of turf, encrusting fleshy (i.e. *Lobophora*) and upright fleshy macroalgae. Ecological interactions and coral demographics (settlement, skeletal extension, partial and whole-colony mortality, corallivory) are explicit and occur at colony scales following probabilistic rules. Grazing maintains macroalgae in a cropped state, which facilitates coral settlement and growth. Acute disturbances include bleaching and cyclones and can occur randomly or following specified scenarios. Their impact on corals is group-specific based on empirical observations. A shift to macroalgal dominance can emerge from insufficient grazing after acute events of extensive coral mortality.

Recently, the model has been developed further to integrate a population model of crown-of-thorns starfish and *eReefs* outputs to simulate spatially-explicit impacts of water quality on corals (suspended sediments) and crown-of-thorns starfish (chlorophyll concentrations) demographics, spatially-realistic regimes of disturbances for the Reef (cyclones, bleaching and crown-of-thorns starfish outbreaks) and connectivity in larval dispersal of coral and crown-of-thorns starfish (Hock et al. 2014, 2017).

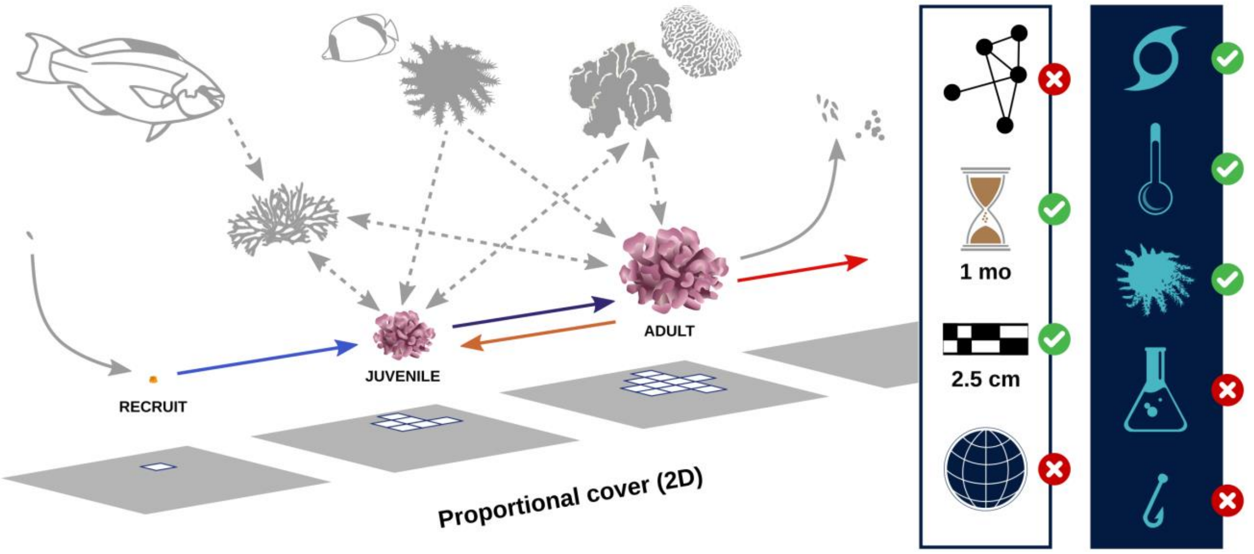
Strengths: Model is stochastic and comprehensive, which allows users to evaluate how changes to a wide range of processes will influence outcomes. Fully spatially-realistic and integrates larval connectivity, *eReefs* outputs for water quality, explicit crown-of-thorns starfish demographics allowing simulation of crown-of-thorns starfish outbreaks and other stressors (cyclones, bleaching). Also enables emergence of coral-algal phase shifts.

Weaknesses: The complexity precludes use by a variety of users although a version is being created for wider dissemination. Does not yet include the effects of acidification or adaptation.

Model outputs: Coral cover (total and per group), abundance of coral juveniles and adults, coral colony size distribution, cover of turf and macroalgae, crown-of-thorns starfish density.

4.2 Compete ©

Johnson 2007, Wakeford et al. 2008



Description: Compete© (Johnson 2007) is a spatially-explicit, individual-based model that simulates sessile modular organisms competing for space on a spatial grid (cellular automaton). Each cell of the grid represents an area either free of colonization or covered by a given class of organism. Probabilistic rules drive the evolution of each cell following demographic processes (recruitment, growth, mortality), the outcome of ecological interactions (competition) with the surrounding environment (neighboring cells) and the impact of external disturbances (mortality).

Wakeford et al. (2008) used Compete© to investigate the impact of acute disturbances on coral cover and community composition at Lizard Island. This study employed a 8m × 4m grid with 2.5cm × 2.5cm cells and 14 hard coral and 3 soft coral species. Demographic rates, outcomes of competition and mortality caused by acute disturbances (coral bleaching, cyclone and crown-of-thorns starfish) were derived from in situ observations. Simulations reproduced the evolution of community composition observed at Lizard Island for the period 1981-2003. The model was then used to explore the relative importance of each ecological process in the observed dynamics and to investigate the role of various regimes (i.e. frequencies) of acute disturbances.

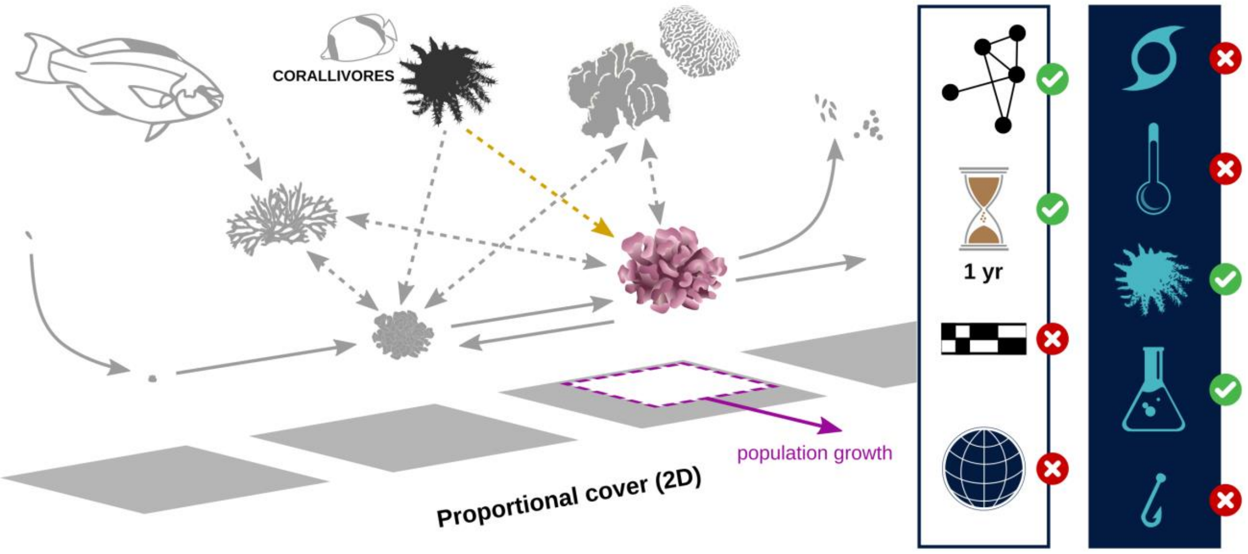
Strengths: Realistic modeling of benthic competition at fine spatial scale (cm) for the study of population and community dynamics and the role of disturbance.

Weaknesses: Parametrised only for Lizard Island. Would need considerable data to inform parameters if applied across the Reef. Not designed to model reef health across landscapes.

Model outputs: Coral cover (total and per group), coral abundance, colony size distribution.

4.3 Model of crown-of-thorns starfish-corals (I): CotSim

Scandol and James 1992, Scandol 1993, 1999, Fabricius et al. 2010



Description: CotSim is a computational model and software developed by Scandol (1993, 1999) that performs simulations of outbreaks of crown-or-thorns starfish populations across the Reef and estimates the consecutive impacts on corals through predator-prey relationships. It combines a size-structured crown-of-thorns starfish demographic model with one or two competing coral (fast and slow growing) populations. Population growth of corals follows a logistic curve but parameter values are not specified. CotSim is spatially structured for the Reef at a reef-by-reef scale with the larval dispersal of crown-of-thorns starfish following patterns predicted by a hydrodynamic model (Dight et al. 1990, Scandol and James 1992). The model is stochastic and was first proposed as an interactive gaming software (Scandol 1999) to let reef managers simulate the propagation of crown-of-thorns starfish populations outbreaks across the Reef and testing the impacts of crown-of-thorns starfish removal on selected reefs. While it is unclear whether this software is still maintained or not, the core model was presumably used by Fabricius et al. (2010) to explore the temporal dynamics and spatial patterns of crown-of-thorns starfish outbreaks as a response to chlorophyll *a* concentrations in the water column. For this application, the dynamics of crown-of-thorns starfish and coral populations were simulated across 321 reefs of the central and northern Reef using a different model of larval dispersal (James et al. 2002). The combined models of crown-of-thorns starfish populations, coral growth, chlorophyll concentrations and larval dispersal were programmed in R. While this model has not been tested against field data, it provides a useful modeling framework to investigate the spatio-temporal distribution of crown-of-thorns starfish driven by chlorophyll concentrations and availability of corals for consumption.

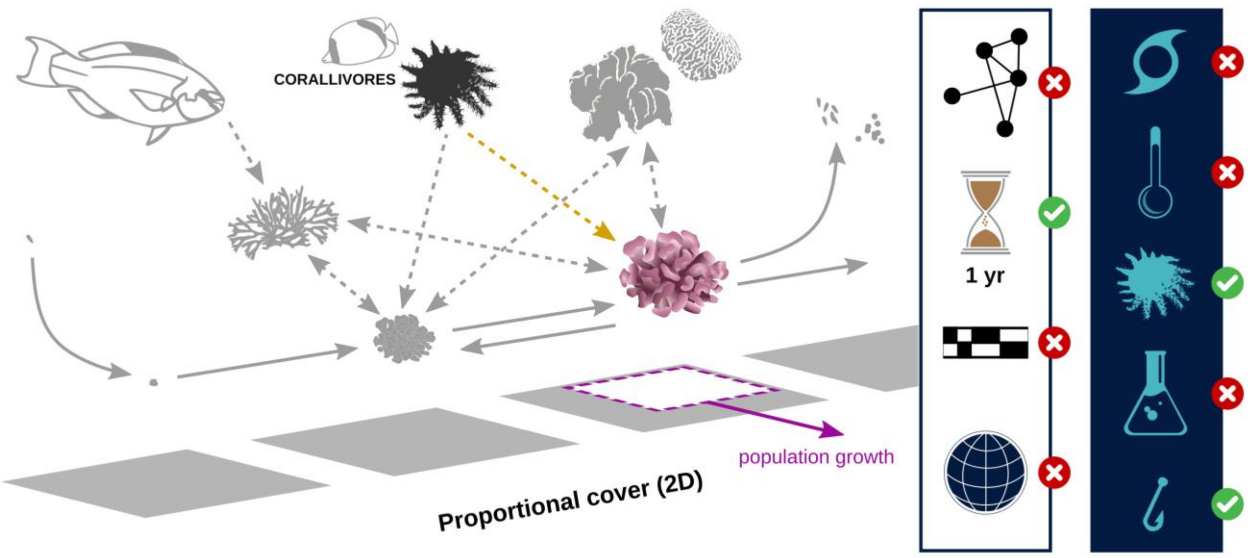
Strengths: Realistic modeling of crown-of-thorns starfish dynamics and consumption on corals. Interactive tool with user-friendly interface allowing managers to envision the propagation of crown-of-thorns starfish outbreaks across reefs connected by larval dispersal. crown-of-thorns starfish removal can be simulated on reefs selected by the user in order to explore the efficiency of tactical control options.

Weaknesses: Coral demographics suffer from a lack of realism. Population growth (logistic) of corals is modeled using unspecified parameters. Would need to be linked to additional models to capture broader reef responses to different environments and stressors.

Model outputs: Crown-of-thorns starfish density per size class, cover of fast and slow growing corals.

4.4 Model of crown-of-thorns starfish-corals (II)

Morello et al. 2014



Description: Similar to Scandol (1993, 1999), this model simulates predator-prey relationships between crown-of-thorns starfish and corals to reproduce the temporal dynamics of crown-of-thorns starfish outbreaks. Here again, two populations of corals are considered (fast and slow growing) and their dynamics are modeled using a logistic growth reduced by mortality due to predation by crown-of-thorns starfish. Fast-growing corals have a 5-fold higher carrying capacity and intrinsic growth rate than slow-growing corals. Coral populations are expressed as biomass but can seemingly be converted to proportional cover. Coral parameters (intrinsic growth rate, carrying capacity and biomass-cover conversion) are arbitrary and the primary focus of the model is to provide a realistic representation of crown-of-thorns starfish dynamics and impacts on corals. Model was fitted to available time series (1994-2011) of crown-of-thorns starfish abundance and coral cover from Lizard Island in order to estimate critical parameters of crown-of-thorns starfish dynamics (crown-of-thorns starfish mortality, relation stock-recruitment, immigration and consumption on corals). This calibration has not been validated yet with an independent data set.

One original feature of the model is the integration of predators of adult and juvenile crown-of-thorns starfish (large fish predators and mobile invertebrates, respectively), a link to fishing, and a specific term for simulating the impact of management intervention (e.g. manual removal). The parameters underlying the effects of predation on crown-of-thorns starfish (including manual removal) remain arbitrary without calibration data. While the model currently lacks a spatial structure and does not integrate disturbances such as cyclones or bleaching, it can be used to explore abstract scenarios of crown-of-thorns starfish control by changing the intensity and efficiency of predation and manual removal.

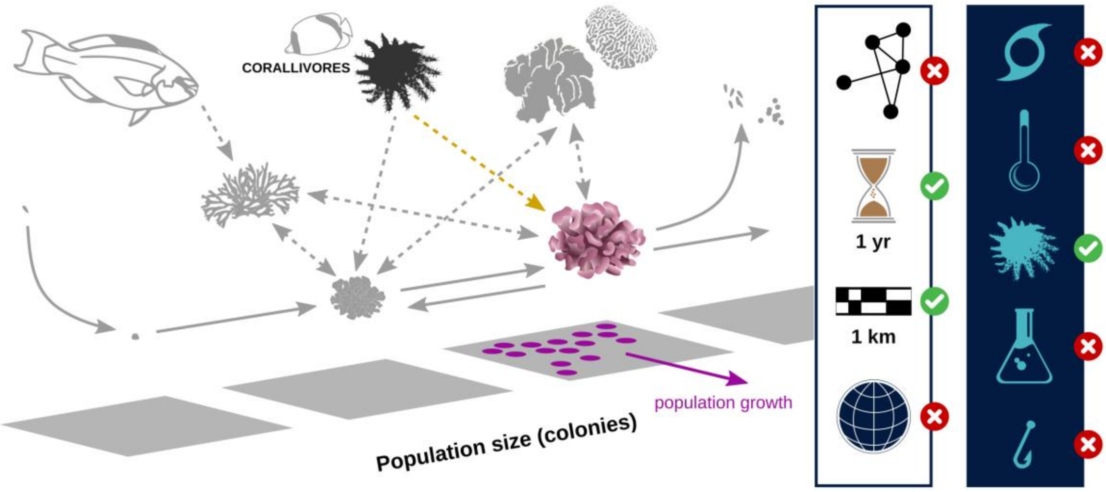
Strengths: Realistic modeling of crown-of-thorns starfish dynamics and consumption on corals. Includes predators of crown-of-thorns starfish and link to fishing.

Weaknesses: Coral demographics suffer from a lack of realism. Coral growth is logistic but expressed as biomass with arbitrary parameters. The two coral populations do not compete for space. The model lacks spatial structure and would need to be linked to additional models to capture broader reef responses to different environments and stressors.

Model outputs: Crown-of-thorns starfish abundance (3 age classes), cover/biomass of fast and slow growing corals, abundance/biomass of predators of crown-of-thorns starfish.

4.5 Model of crown-of-thorns starfish-corals (III)

Mellin et al. 2016



Description: This model combines demographic models of crown-of-thorns starfish and corals with species distribution models to simulate crown-of-thorns starfish outbreaks and their propagation across an artificial seascape. The model is a cellular automaton with a 100 × 100 grid where every cell (1km × 1km) can host a coral and a crown-of-thorns starfish population. Each cell is assigned an index of habitat suitability which locally affects the carrying capacity of coral/crown-of-thorns starfish population. Population growth is modeled by a linear function whereby the intrinsic growth rate takes random values from a specified normal distribution. There is no density-dependence in growth, but intrinsic growth rates are forced to take negative or positive values around carrying capacity to mimic stability and avoid population overgrowth. Corals are modeled as individual colonies, and the consumption of corals by crown-of-thorns starfish follows a Lotka-Volterra predator-prey model (i.e. with no density-dependence in consumption).

The model is used as a “proof-and-concept” to demonstrate how integrating models of habitat suitability with simple demographics and ecological interactions increase our ability to forecast marine invasions (e.g. crown-of-thorns starfish outbreaks) under climate change. Crown-of-thorns starfish can disperse across the seascape following a specified function that determines the direction and distance of dispersion. Populations are simulated across various seascape configurations (i.e. distribution of habitat suitability index) and under abstract scenarios of climate change, which progressively affect habitat suitability across some predefined spatial gradients.

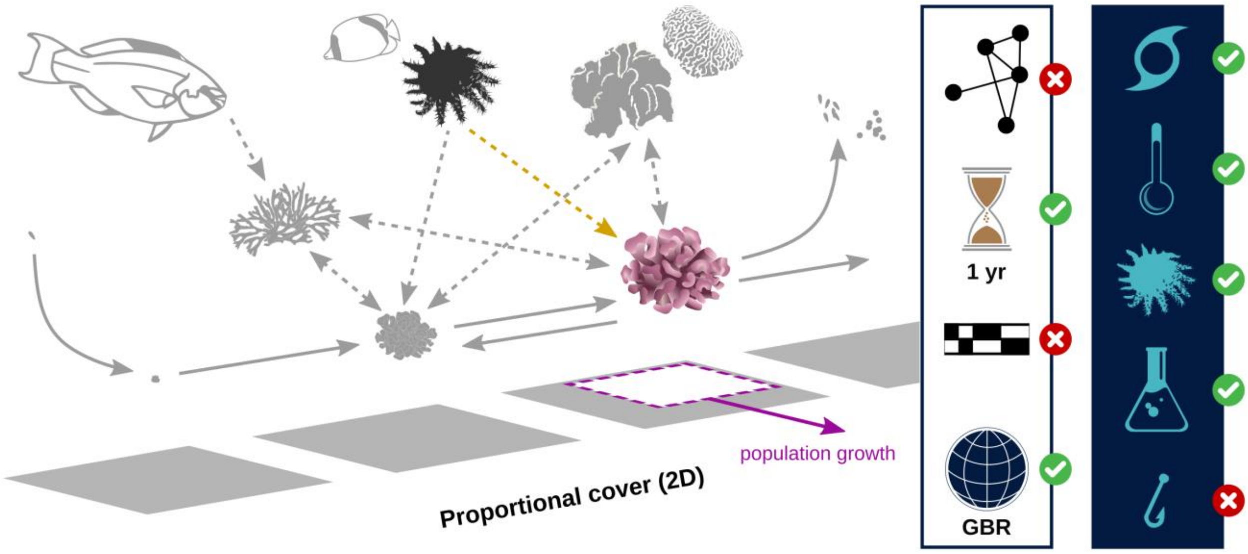
Strengths: Integration of habitat suitability into coral and crown-of-thorns starfish demographics. Explicit function of crown-of-thorns starfish dispersion.

Weaknesses: Coral demographics suffer from a lack of realism: linear population growth, carrying capacity expressed as a number of colonies. Converting number of coral colonies into cover requires assumptions about colony size. Would need implementation of a spatial structure integrating external impacts (cyclones, bleaching) and realistic patterns of larval dispersal across the Reef. Requires quantitative links between coral habitat suitability and parameters of population growth.

Model outputs: Crown-of-thorns starfish and coral colony abundance over time and space.

4.6 Empirical (logistic) model of coral recovery

Mumby and Anthony 2015, Wolff et al. 2016, 2018



Description: This is a simple logistic growth model parameterised with empirical observations of the recovery dynamics of *Acropora* cover in the southern Reef (Halford et al. 2004). The model can be used to simulate coral cover over time, assuming *Acropora* accounts for most of the hard-coral dynamics on the Reef (Osborne et al. 2011). Specifically, it has been used to assess reef vulnerability across the Reef in response to climate change scenarios (Wolff et al. 2018). Here, the Reef was abstracted by 1,312 reef polygons (4km × 4km), each being informed by probabilistic exposure to different stressors: cyclones, thermal stress (bleaching), crown-of-thorns starfish outbreaks and elevated nutrient concentrations which decrease the thermal tolerance of corals. Disturbance impacts were parameterised based on observed mortality rates. The logistic model of coral dynamics was run for each reef polygon with the associated impact probabilities following scenarios of climate change projections (2017-2050) in order to assess the vulnerability of reefs and the potential for management to mitigate impacts.

While the population model is deterministic, the occurrence of disturbances is stochastic, and this generates uncertainty to the predicted coral cover. Typically, a reef simulation is run multiple times to capture stochasticity in the predicted trajectory. As for other simple population models, individual-level mechanisms that contribute to the rate of change in coral cover are not explicit. The implication is that a single model of population growth (i.e. with invariant parameters) will predict the same cover increment (for a given cover value), while recovery rate is likely to vary across the Reef with spatial variations in recruitment, colony growth and background mortality.

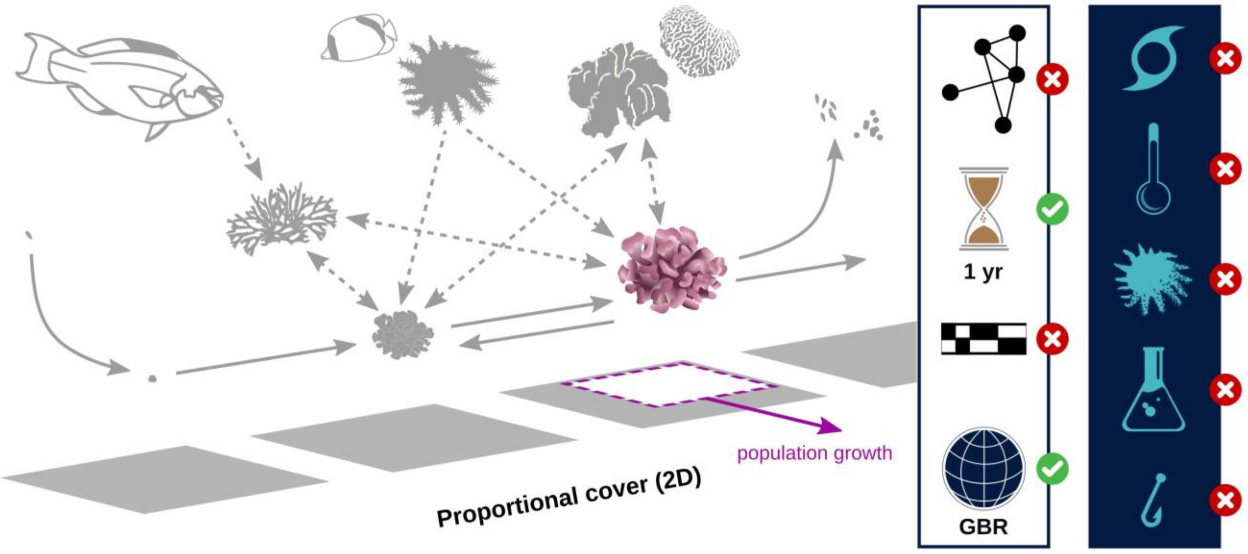
Strengths: Dynamics of coral cover derived from empirical observations. Spatially-explicit regimes of cyclones, bleaching, crown-of-thorns starfish outbreaks following 4 climate change scenarios.

Weaknesses: Rate of change in coral cover is representative of southern Reef but may vary with environmental gradients, community composition, essentially any variation in the intensity of individual-level mechanisms that underlie the dynamics of coral cover. Currently not designed to integrate larval dispersal (connectivity) as this would require changing recovery rate.

Model outputs: Coral (*Acropora*) cover over time and space.

4.7 Empirical (Gompertz) model of coral recovery

Osborne et al. 2017



Description: In a recent study, (Osborne et al. 2017) parameterised models of coral recovery based on modified Gompertz equations (a sigmoid growth curve similar to the logistic function) with observations of coral cover collected on 42 reefs in the Reef from 1994 to 2009. Recovery models were fit separately for Acroporidae and other hard corals, and a Bayesian framework permitted the propagation of uncertainty to predictions of total coral cover from the separate growth estimates.

While this analysis was essentially descriptive, reporting changes in recovery rates over the studied period, the parameterised models of coral recovery could be used as predictive models of coral cover if combined with modeled impacts of acute disturbances, such as cyclones, bleaching and crown-of-thorns starfish. It is unclear, however, whether recovery rates were parameterised separately for each surveyed region of the Reef. The temporal changes in coral recovery evidenced in this study (here attributed to increasing sea surface temperatures) highlight the limits of applying a single population model across environmental gradients. Unlike the logistic growth model of *Acropora* (Mumby and Anthony 2015), Gompertz models are available for two coral groups (fast- and slow-growing corals), which offers greater realism to the modeling of total coral cover.

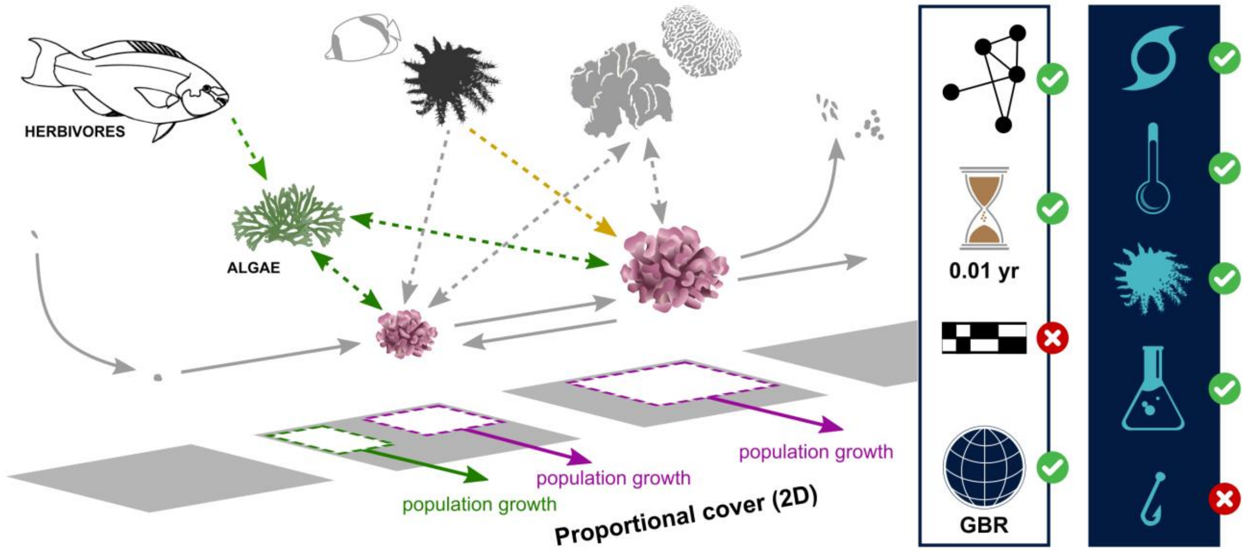
Strengths: Separate models of recovery for fast- and slow-growing corals. Explicit (statistical) modeling of uncertainty in the trajectory of coral cover.

Weaknesses: Unclear whether or not model parameterisation differs among Reef regions. Would require integration of external impacts from spatially-realistic regimes of acute disturbances (cyclones, bleaching, crown-of-thorns starfish). Unclear how to integrate larval dispersal as this would require changing recovery rate.

Model outputs: Coral (Acroporidae, other corals) cover over time.

4.8 Model of coral-algal interactions I (Home)

McCook et al. 2001; Wolanski et al. 2003, 2004; Wolanski and De'ath 2005



Description: This is an analytical model of corals and algae competing for space under the control of herbivorous fish. The reef is represented by a system of 4 ordinary differential equations (ODE) that give the dynamics of juvenile corals, adult corals, algae and herbivorous fish. Competition for space is modeled using Lotka-Volterra-type equations where population growth is logistic. External disturbances are modeled as acute impacts from rain-generated river plumes and cyclones. River flood plumes increase suspended sediment concentration which affect fish grazing, algal growth, coral recruitment and coral survival. High nutrient concentrations increase algal growth. Cyclones affect the cover of adult corals and algae. Wolanski and De'ath (2005) augmented the model with population dynamics of the crown-of-thorns starfish following Scandol and James (1992) and bleaching projections.

One originality is that the ecological model is coupled with a hydrodynamic model allowing simulation of river plumes' movement following past flood events in the Reef. The hydrodynamic model also enables simulation of larval dispersal thus creating coral connectivity among reefs. Model predictions of coral cover seem to compare favorably with Reef observations, especially after integrating the impacts of crown-of-thorns starfish outbreaks.

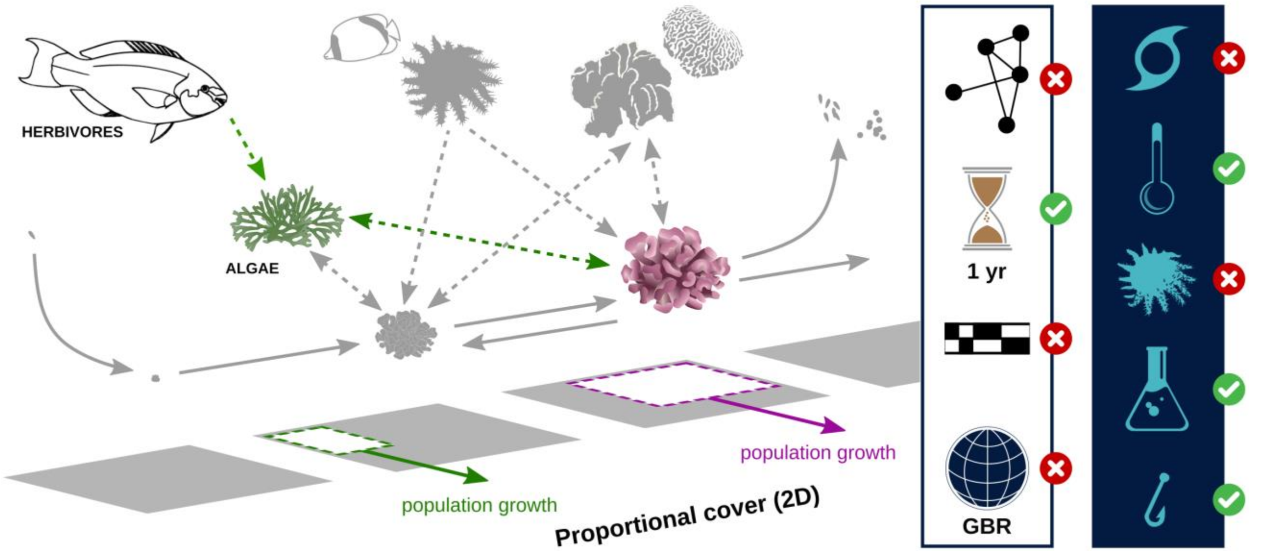
Strengths: Coupled ecological-hydrodynamic model with explicit impacts of nutrients and suspended sediments and emergence of coral-algal phase shifts. Juvenile and adult corals are modeled separately allowing integration of larval connectivity with local recruitment.

Weaknesses: Would require integration of more recent spatial scenarios of climate warming.

Model outputs: Cover of adult and juvenile corals, algal cover, density of adult crown-of-thorns starfish.

4.9 Model of coral-algal interactions II

Mumby et al. 2007, Anthony et al. 2011, Blackwood et al. 2012, Bozec et al. 2013



Description: This model was initially developed by (Mumby et al. 2007) to explore the dynamics of coral-algal phase shifts in the Caribbean. A reef system is represented by 2 ODE (corals and macroalgae) and the focus is on coral-algal competition under the control of grazing. The model was later augmented with one equation for herbivorous fish (Blackwood et al. 2012) and the integration of structural complexity and impacts on grazing (Bozec et al. 2013). The model was applied to the Reef by Anthony et al. (2011) using a specific parameterisation and the introduction of various disturbance impacts: bleaching, nutrients (affecting macroalgal growth), ocean acidification (affecting coral growth/calcification). Model simulations were used to explore the persistence of coral-dominated reefs for various scenarios of water chemistry and sea surface temperatures representative of climate change projections.

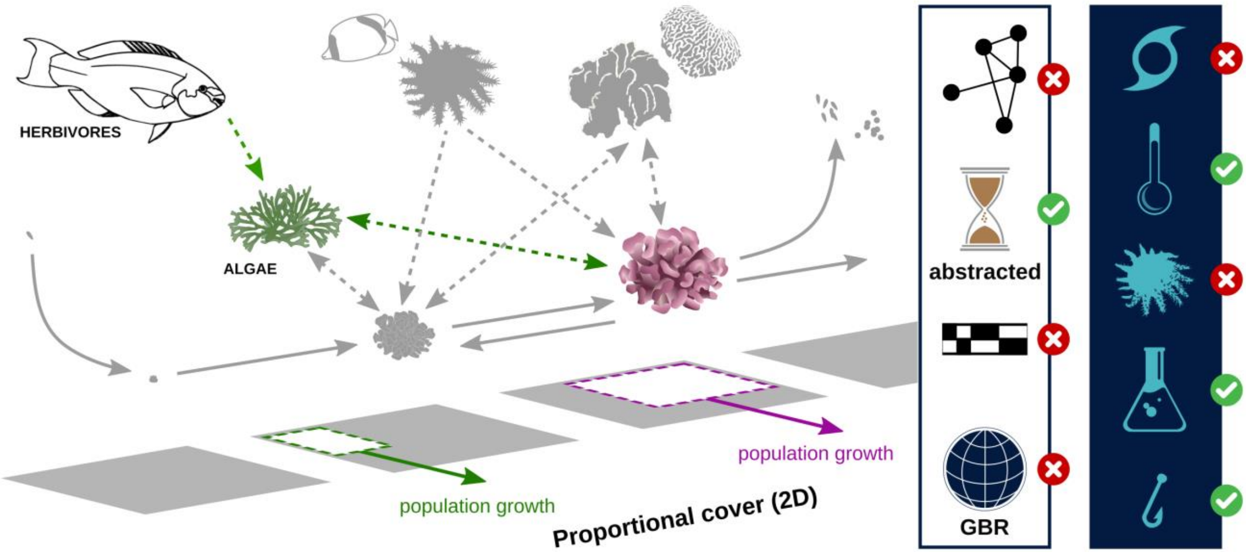
Strengths: Integrates impacts of ocean acidification on coral-algal competition and coral persistence.

Weaknesses: Model remains essentially descriptive in the absence of a realistic spatial framework. Model cannot easily integrate larval connectivity and impact on coral recruitment.

Model outputs: Coral and macroalgal proportional cover.

4.10 Model of coral-algal interactions III

van de Leemput et al. 2016, Hughes et al. 2017



Description: This is a very similar model to the one developed by (Mumby et al. 2007) with the addition of an equation for modeling the dynamics of herbivorous fish and grazing as in (Blackwood et al. 2012). Model equations also include specific feedback mechanisms whose impacts are explored on system dynamics and coral persistence. The model was also used to illustrate how a range of management options can target different components of a reef system (drivers, thresholds and feedbacks) to maintain coral persistence under a changing climate (Hughes et al. 2017). Here, the following external impacts were integrated into the system: nutrients affecting algal growth, climate change enhancing coral mortality and fishing decreasing herbivore populations.

This model remains essentially descriptive because of the use of abstract demographic rates and external impacts, and the absence of a spatial context. The model provides, however, a theoretical framework to envision the complexity of ecological interactions and the importance of feedbacks for the dynamics of coral-algal phase shifts.

Strengths: Illustrate the importance of feedbacks to understand the dynamics of coral-algal phase shifts and foresee the possible pathways of management intervention.

Weaknesses: Model is essentially descriptive in the absence of a realistic spatial framework and empirically-derived demographic rates.

Model outputs: Coral and macroalgal cover, herbivore abundance proportional to carrying capacity.

4.11 Model of carbon budget

Johnson et al. 1995

Description: The model is a steady-state representation of a carbon flux network for a typical mid-shelf reef on the Reef. Using empirical data from Davies Reef, the model quantifies the multiple pathways that connect 19 living (from bacteria to predatory fishes) and non-living (detritus) compartments. Corals are separately represented by zooxanthellae and coral polyps, with a flow representing organic carbon produced by photosynthesis and translocated to the host, and a flow from coral polyps to fish representing corallivory. The network is parametrised to describe two community states: before and after a hypothetical shift from coral to algal (turf) dominance. The resulting networks are compared using specific metrics derived from network analysis, enabling the exploration of the impacts of coral-to-algal phase shift on system trophodynamics.

Strengths: Model quantifies main pathways of organic carbon and characterise system trophodynamics for different community states.

Weaknesses: Model is static, not spatial, and does not inform about changes in proportional cover of sessile organisms. Does not integrate impact of acute disturbances.

Model outputs: Carbon flux through 19 compartments, network metrics.

4.12 Model of coral polyp in *eReefs*

Baird et al. 2013, Gustafsson et al. 2013, Mongin and Baird 2014, Mongin et al. 2016

Description: The *eReefs* hydrodynamic-biogeochemical modeling system integrates a model of coral growth that is linked to daily predictions of ambient light, nutrients and particulate organic across the Reef. This model combines a growth model of zooxanthellae with a model of interaction host-symbiont. Corals are represented by the biomass of living tissue and that of zooxanthellae, and are allowed to grow following the availability of particulate matter (heterotrophy) and the translocation from zooxanthellae of organic matter produced by photosynthesis (autotrophy). The model is a complex set of equations describing the mechanisms involved in coral growth and produces a daily estimate of coral living biomass (in gram of nitrogen per m^2) across the Reef at 1km and 4km resolutions. The model also estimates rates of calcification as a function of polyp biomass and ambient levels or aragonite saturation.

Strengths: Sophisticated modeling of coral physiology with explicit link to the physical and biogeochemical environment. Produces spatial layers of daily predictions of coral tissue biomass and calcification that integrate the effects of various stressors (water quality, temperature).

Weaknesses: While there is potential to predict the cumulative effects of various physiological stressors, the model does not offer a formal link with ecological processes and coral cover.

Model outputs: Spatial layers (1km and 4km resolutions) of daily estimates of coral polyp and zooxanthellae biomass, rates of coral calcification and dissolution.

4.13 Model of coral energy budget

Anthony and Connolly 2004, Anthony et al. 2009

Description: This is a model of coral energetics that estimates the daily energy balance of coral symbiosis approximated by daily rates of photosynthesis, respiration and heterotrophy. Energy balance can be calculated from ambient values of temperature, light (irradiance) and turbidity, and enables estimation of the size of energy storage (as lipid content) over a given period of time. The dynamics of energy reserves are then used to determine coral survival in a per cent

given environment. Specifically, the model allows estimating the risk of mortality following bleaching, depending on whether or not a positive or negative energy balance is maintained over time. A negative energy balance is attained when maintenance costs exceed carbon acquisition, thus increasing the risk of mortality. The model was calibrated using experimental data (Anthony et al. 2009) and offers predictions of coral mortality as determined by bleaching severity and duration, heterotrophy and the size of energy reserves before bleaching.

Strengths: Prediction of mortality risk following bleaching from core mechanisms of coral physiology. Captures cumulative effects of stress with survival being dependent on the amount of lipid reserves accumulated before stress and the rate by which these reserves are depleted in the absence of photosynthetic activity (i.e. bleached state).

Weaknesses: Model predicts mortality but not coral demographics. Model needs inputs from a realistic, physical (light, temperature, turbidity) environment (e.g, *eReefs* layers).

Model outputs: Daily energy balance and size of energy stores.

5.0 Synthesis and recommendations for model integration into RIMReP

A variety of approaches have been applied to model coral dynamics on the Reef. While they differ in various respects, they can be broadly grouped into 3 categories. First, **individual-based coral models** (i.e. where coral individuals are modeled explicitly) are arguably the most complex models as they disaggregate coral demographics into their component mechanisms: settlement, skeletal extension, partial and whole colony mortality, competition, and predation. The most comprehensive model to date applied to the Reef is Reefmod (Mumby et al. 2007, Ortiz et al. 2014). Then, there is a large group of **models of coral population growth** which are essentially models of recovery of coral cover (Scandol 1999, Morello et al. 2014, Mumby and Anthony 2015, Mellin et al. 2016, Mellin et al. 2018 – Supplementary Report S4, Osborne et al. 2017). Such models describe temporal changes in coral cover following a specific function (generally sigmoidal). The last group is formed by **combined models of coral-algal populations** (McCook et al. 2001, Mumby et al. 2007, van de Leemput et al. 2016), which focus on coral-algal competitions and allow emergence of coral-algal phase shifts. Most of these models allow integration of one or multiple disturbances (**Table 2**). Models not included in these (i.e. physiological models, carbon flux model) have a focus that makes them less suitable to describe or predict changes in coral cover across the Reef.

We highlight below some aspects that should be considered for comparing the capacity of these models to capture reef status and trends.

- Dynamic models of population growth essentially represent reefs where coral cover persists and invariably recovers from acute disturbances. For a given parameterisation, coral cover will always recover with the same dynamics (i.e. at the same rate). This precludes the emergence of shifts in coral population dynamics, which might occur in a changing environment or with fluctuating larval supply. In particular, coral-algal phase shifts are precluded from this modeling approach. Moreover, using present-day recovery rates to predict reef futures may generate unrealistic scenarios of climate change.
- Using a single parameterisation for the growth function is unlikely to reflect the range of reef environments of the Reef. The intensity of demographic processes, such as coral recruitment or background mortality under chronic stress, is likely to vary considerably across the system. Moreover, geographic or habitat differences in community composition likely result in different coral cover dynamics. Identifying typical recovery curves for a set of representative regions/habitats (e.g. following latitude and shelf-position) is a prerequisite to capture the variability of recovery dynamics across the Reef.
- Models that integrate coral-algal competition explicitly (i.e. Reefmod and models of coral-algal populations) are more likely to produce a greater variety of coral dynamics because the population growth is partially dependent on algal dynamics. Such models generally capture the propensity of a system to shift from coral to algal dominance.
- Models that include explicit recruitment (e.g. Home, Reefmod) or other demographic mechanisms (e.g. juvenile growth and survival, competition among corals such as in Reefmod) would capture even more complex dynamics of coral recovery.
- Only few models (Home, Reefmod) integrate an explicit formulation of coral recruitment in a spatial context (i.e. with explicit larval dispersal). While larval connectivity among Reef reefs can be informed by hydrodynamic models, linking model-based estimates of larval supply to realistic rates of coral recruitment remains a considerable challenge.
- Most models can integrate the effects of cyclones, bleaching and crown-of-thorns starfish, by imposing a loss of coral cover at a given time. Most important is how acute disturbance impacts are parameterised which implies to specify (1) when an acute disturbance occurs and (2) the magnitude of the associated coral loss. Very few models (Wolff et al. 2018)

support their predictions of acute disturbances from spatially-explicit empirical data. Simulations can be informed by historical cyclone tracks (Wolff et al. 2016) and surface temperatures (Hock et al. 2017) but the reproduction of crown-of-thorns starfish outbreaks is challenged by the scarcity of data. Here, demographic model of crown-of-thorns starfish might be used to simulate outbreak propagation. Impacts from acute disturbances should follow empirical observations but few models actually do this (Reefmod, Compete, Home, model of Mumby and Anthony 2015).

- Only few models integrate the impact of water quality on corals [Home and the model of Mumby and Anthony (2015) in Wolff et al. (2018), see also Mellin et al. 2018]. A recent version of Reefmod applied to the Cairns management region integrates the effects of suspended sediments on demographic processes of corals based on recent experimental data.
- Fishing has been integrated in two ways: (1) effects on fish predators of crown-of-thorns starfish (as in Morello et al. 2014) which releases predation on crown-of-thorns starfish and consecutively increases coral mortality, and (2) effects on fish herbivores (as in Reefmod), which decreases grazing intensity and can ultimately lead to macroalgal overgrowth. This latter effect is not an issue for the Reef where herbivorous fish are not harvested. This might explain why fishing is generally discounted (e.g. Wolanski et al. 2004).
- In general, selecting several models rather than a single one is more profitable to decision-making. A multi-model approach is more likely to capture different properties of the modeled system and a broader range of responses to disturbances. Moreover, using distinct models to simulate a specific management scenario generates a range of possible outcomes (i.e. model uncertainty) that is informative to the decision-making process.

Not all models have the capacity to address management priorities relevant to the Reef (**Table 3**). We consider here a range of management questions that require simulation of realistic scenarios of interventions, at least at a reef-by-reef scale, in order to inform decision-making:

- **climate change predictions**: ability to project scenarios of future bleaching events.
- **water quality**: ability to simulate spatial scenarios of changing concentrations of sediments, nutrients, chlorophyll, pesticides on corals, algae and/or crown-of-thorns starfish.
- **crown-of-thorns starfish control**: ability to simulate across space realistic scenarios of crown-of-thorns starfish culling.
- **coral-algal phase shifts**: capacity to predict algal phase shifts after acute disturbance.
- **reef restoration**: ability to explore scenarios showcasing the feasibility of novel techniques to help repairing coral damages or adapting to future thermal stress.
- **spatial prioritisation of management**: ability to define optimal spatial strategies.

Table 2. Summary of the 13 model of Great Barrier Reef coral dynamics with the different types of disturbance implemented. Grey colored rows designate models that are not further considered (Table 3) due to their limited potential for management scenario analysis. The last column refers to implementation characteristics with an indication of model maturity (D=developmental, M=mature) followed by computational requirements (see also Appendix 1).

Model designation	Acronym	References	🌀	🌡	✳	⚗	🪝	🔧
Reefmod	Reefmod	Mumby et al. 2007, 2014; Ortiz et al. 2014; Bozec et al. 2015, 2016	✓	✓	✓	✓	✓	D, *MATLAB*
Compete©	-	Johnson 2007; Wakeford et al. 2008	✓	✓	✓	✗	✗	M, software
Model of crown-of-thorns starfish-corals I	CotSim	Scandol 1993, 1999; Fabricius et al. 2010	✗	✗	✓	✓	✗	M, software
Model of crown-of-thorns starfish-corals II	MCC-II	Morello et al. 2014	✗	✗	✓	✗	✓	D
Model of crown-of-thorns starfish-corals III	MCC-III	Mellin et al. 2016	✗	✗	✓	✗	✗	D, *R*
Empirical (logistic) model of coral recovery	EM-Logistic	Mumby and Anthony 2015; Wolff et al. 2016, 2018	✓	✓	✓	✓	✗	D, *MATLAB*
Empirical (Gompertz) model of coral recovery	EM-Gompertz	Osborne et al. 2017	✗	✗	✗	✗	✗	D, *R*
Model of coral-algal interactions I (Home)	Home	McCook et al. 2001; Wolanski et al. 2003, 2004	✓	✓	✓	✓	✗	M
Model of coral-algal interactions II	MCA-II	Mumby et al. 2007; Anthony et al. 2011	✗	✓	✗	✓	✓	D, *MATLAB*
Model of coral-algal interactions III	MCA-III	van de Leemput et al. 2016; Hughes et al. 2017	✗	✓	✗	✓	✓	D
Model of carbon flux	-	Johnson et al. 1995	✗	✗	✗	✗	✗	D
Model of coral polyp in *eReefs*	-	Baird et al. 2013; Gustafsson et al. 2013; Mongin and Baird 2014	✗	✓	✗	✓	✗	M, web portal
Model of coral energy budget	-	Anthony and Connolly 2004; Anthony et al. 2009	✗	✓	✗	✓	✗	D, *MATLAB*

Table 3. Models ability to inform decision-making by simulating specific scenarios of reef management relevant to the Great Barrier Reef

Scope for management	Not captured	Abstracted	Realistically reproduced
Climate change projections	CotSim MCC-II EM-Gompertz Home MCA-III	MCC-III MCA-II	**Reefmod**: 4 scenarios (RCP 2.6, 4.5, 6.0 and 8.5) based on SST projections of climate change model HadGEM2-ES with calculation of degree heating month (Wolff et al. 2015); projections downscaled using past DHM of the Reef (Hock et al. 2017). **EM-Logistic**: same data layers.
Effects of water quality	MCC-II MCC-III EM-Gompertz	MCA-II MCA-III	**Reefmod**: Impacts of spatially-realistic (*eReefs*) reductions of suspended sediments on corals (juvenile mortality, larval survival) and nutrients (turf and macroalgae); Impacts of spatially-realistic (*eReefs*) reductions of Chl on crown-or-thorns starfish outbreak initiation. **CotSim**: Impacts of reductions of Chl on crown-of-thorns starfish outbreak initiation. **EM-Logistic:** Impacts of reduction of nutrients on algae **Home:** Impacts of reduction of nutrients on algae, impacts of sediments on coral settlement and survival.
Crown-of-thorns starfish control	EM-Logistic EM-Gompertz Home MCA-II MCA-III	CotSim MCC-II MCC-III	**Reefmod**: Define the most efficient spatial allocation of control effort. Explore various effort allocations, informed by surveys, reef health or connectivity.
Coral-algal phase shifts	CotSim MCC-II MCC-III EM-Logistic EM-Gompertz	MCA-II MCA-III	**Reefmod**: Probability of coral-algal phase shifts across reefs; can link with biomass of fish herbivores. **Home**: Spatial predictions of coral and algal cover.
Reef restoration: repair	CotSim MCC-II MCC-III EM-Logistic EM-Gompertz	MCA-II MCA-III	**Reefmod**: Explore trade-offs between cost of coral transplantation or substratum stabilisation and impact on reef recovery; evaluate feasibility of restoration at different spatial scales. **Home**: Simulation possible of coral transplants with a dedicated equation but analysis cost/success difficult without explicit size and density of transplants.
Reef restoration: adaptation	CotSim MCC-II MCA-II MCA-III EM-Logistic EM-Gompertz	MCC-III	**Reefmod**: Explore how stress-tolerant phenotypes can spread across the Reef through local persistence, reproduction and dispersion. **Home**: Simulation possible with a dedicated equation for stress-tolerant genotype but requires coral reproduction to be implemented.
Spatial prioritization	CotSim MCA-II MCA-III Home	MCC-II MCC-III EM-Logistic EM-Gompertz	**Reefmod**: Explore impacts of management intervention across space (coral and crown-of-thorns starfish connectivity) accounting for spatially-realistic scenarios of acute disturbances.

6.0 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.

Anthony, K., J. A. Maynard, G. Diaz-Pulido, P. J. Mumby, P. A. Marshall, L. Cao, and O. Hoegh-Guldberg. 2011. Ocean acidification and warming will lower coral reef resilience. Global Change Biology 17:1798–1808.

Anthony, K. R., and S. R. Connolly. 2004. Environmental limits to growth: physiological niche boundaries of corals along turbidity–light gradients. Oecologia 141:373–384.

Baird, M. E., P. J. Ralph, F. Rizwi, K. Wild-Allen, and A. D. Steven. 2013. A dynamic model of the cellular carbon to chlorophyll ratio applied to a batch culture and a continental shelf ecosystem. Limnology and Oceanography 58:1215–1226.

Blackwood, J. C., A. Hastings, and P. J. Mumby. 2012. The effect of fishing on hysteresis in Caribbean coral reefs. Theoretical Ecology 5:105–114.

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

DeAngelis, D. L., and V. Grimm. 2014. Individual-based models in ecology after four decades. F1000prime reports 6.

DeAngelis, D. L., and S. Yurek. 2017. Spatially explicit modeling in ecology: a review. Ecosystems 20:284–300.

Dight, I., M. James, and L. Bode. 1990. Modelling the larval dispersal of Acanthaster planci. Coral Reefs 9:125–134.

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.

Fabricius, K., 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.

Fulton, E. A., J. S. Link, I. C. Kaplan, M. Savina-Rolland, P. Johnson, C. Ainsworth, P. Horne, R. Gorton, R. J. Gamble, A. D. Smith, and others. 2011. Lessons in modelling and management of marine ecosystems: the Atlantis experience. Fish and Fisheries 12:171–188.

Gustafsson, M. S., M. E. Baird, and P. J. Ralph. 2013. The interchangeability of autotrophic and heterotrophic nitrogen sources in Scleractinian coral symbiotic relationships: A numerical study. Ecological modelling 250:183–194.

Halford, A., A. J. Cheal, D. Ryan, and D. McB. 2004. Resilience to Large-Scale Disturbance in Coral and Fish Assemblages on the Great Barrier Reef. Ecology: 1892–1905.

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., M. L. Barnes, D. R. Bellwood, J. E. Cinner, G. S. Cumming, J. B. Jackson, J. Kleypas, I. A. Van De Leemput, J. M. Lough, T. H. Morrison, and others. 2017. Coral reefs in the Anthropocene. Nature 546:82.

James, M. K., P. R. Armsworth, L. B. Mason, and L. Bode. 2002. The structure of reef fish metapopulations: modelling larval dispersal and retention patterns. Proceedings of the Royal Society of London B: Biological Sciences 269:2079–2086.

Johnson, C., D. Klumpp, J. Field, and R. Bradbury. 1995. Carbon flux on coral reefs: effects of large shifts in community structure. Marine Ecology Progress Series:123–143.

Johnson, C. R. 2007. Compete© An individual-based spatial modelling software to simulate ecological interactions and evolution in sessile organisms. Institute for Marine and Antarctic Studies, University of Tasmania.

van de Leemput, I. A., T. P. Hughes, E. H. van Nes, and M. Scheffer. 2016. Multiple feedbacks and the prevalence of alternate stable states on coral reefs. Coral Reefs 35:857–865.

McCook, L. J., E. Wolanski, and S. Spagnol. 2001. Modelling and visualizing interactions between natural disturbances and eutrophication as causes of coral reef degradation. Oceanographic processes of coral reefs: physical and biological links in the Great Barrier Reef:113–125.

Melbourne-Thomas, J., C. Johnson, P. Alino, R. C. Geronimo, C. Villanoy, and G. Gurney. 2011. A multi-scale biophysical model to inform regional management of coral reefs in the western Philippines and South China Sea. Environmental Modelling & Software 26:66–82.

Mellin, C., M. Lurgi, S. Matthews, M. A. MacNeil, M. Caley, N. Bax, R. Przeslawski, and D. Fordham. 2016. Forecasting marine invasions under climate change: Biotic interactions and demographic processes matter. Biological Conservation 204:459–467.

Mellin, C., K.R.N. Anthony, E. Peterson, C. Ewels, M. Puotinen. 2018. Model to inform the Design of a Reef Integrated Monitoring and Reporting Program (RIMReP). Supplementary Report S4 to Draft report of the Coral Reef Expert Group. Report provided to GBRMPA.

Mongin, M., and M. Baird. 2014. The interacting effects of photosynthesis, calcification and water circulation on carbon chemistry variability on a coral reef flat: a modelling study. Ecological modelling 284:19–34.

Mongin, M., M. E. Baird, B. Tilbrook, R. J. Matear, A. Lenton, M. Herzfeld, K. Wild-Allen, J. Skerratt, N. Margvelashvili, B. J. Robson, and others. 2016. The exposure of the Great Barrier Reef to ocean acidification. Nature communications 7:10732.

Morello, E. B., É. E. Plagányi, 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.

Mumby, P. J., and K. Anthony. 2015. Resilience metrics to inform ecosystem management under global change with application to coral reefs. Methods in Ecology and Evolution 6:1088–1096.

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.

Osborne, K., A. M. Dolman, S. C. Burgess, and K. A. Johns. 2011. Disturbance and the dynamics of coral cover on the Great Barrier Reef (1995–2009). PloS one 6:e17516.

Osborne, K., A. A. Thompson, A. J. Cheal, M. J. Emslie, K. A. Johns, M. J. Jonker, M. Logan, I. R. Miller, and H. Sweatman. 2017. Delayed coral recovery in a warming ocean. Global change biology 23:3869–3881.

Scandol, J., and M. James. 1992. Hydrodynamics and larval dispersal: a population model of Acanthaster planci on the Great Barrier Reef. Marine and Freshwater Research 43:583–595.

Scandol, J. P. 1993. CotSim: Scientific visualisation and gaming-simulation for the Acanthaster phenomenon. Great Barrier Reef Marine Park Authority, Townsville (Australia).

Scandol, J. P. 1999. CotSim—an interactive Acanthaster planci metapopulation model for the central Great Barrier Reef. Marine Models 1:39–81.

Wakeford, M., T. Done, and C. Johnson. 2008. Decadal trends in a coral community and evidence of changed disturbance regime. Coral Reefs 27:1–13.

Weijerman, M., E. A. Fulton, I. C. Kaplan, R. Gorton, R. Leemans, W. M. Mooij, and R. E. Brainard. 2015. An integrated coral reef ecosystem model to support resource management under a changing climate. PLoS one 10:e0144165.

Wolanski, E., R. H. Richmond, and L. McCook. 2004. A model of the effects of land-based, human activities on the health of coral reefs in the Great Barrier Reef and in Fouha Bay, Guam, Micronesia. Journal of Marine Systems 46:133–144.

Wolanski, E., R. Richmond, L. McCook, and H. Sweatman. 2003. Mud, marine snow and coral reefs: the survival of coral reefs requires integrated watershed-based management activities and marine conservation. American Scientist 91:44–51.

Wolanski, E. and De'ath, G. 2005. Predicting the impact of present and future human land-use on the Great Barrier Reef. Estuarine, Coastal and Shelf Science, 64, 504-508.

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.

7.0 Appendix 1

Model	Description	Scope	Detail	Purpose	Spatial structure	Spatial connectivity	Time resolution	Parametrisation	State variables	Coral demographic processes	Coral disturbances	Modelling environment
REEFMOD Mumby et al. 2007, Ortiz et al. 2014, Bozec et al. 2015, 2016	Computational	Applied; predictive	Individual-based; stochastic	Simulate coral and CoTS populations across the GBR; Explore scenarios of coral persistence	Spatially-explicit (1-400 m^2) Spatially-structured (reef)	CoTs / Coral connectivity (Hock et al. 2014, 2017)	6 month	Palau + GBR	Colony size of 6 coral groups + patch size of 4 algal (EAM, thick turf, Lobophora, upright fleshy) + density of CoTS (8 age classes)	Colony growth; partial and whole colony mortality; coral predation; settlement; grazing; coral-algal competition; coral reproduction	Cyclones; bleaching (whole-colony and partial mortalities); suspended sediments; Chlorophyll; CoTS; nutrients (algal growth)	MATLAB Reefmod version 5.5 (2018)
COMPETE© Johnson 2007, Wakeford et al. 2008	Computational	Applied; predictive	Individual-based; stochastic	Explore species interactions and persistence of taxonomic composition	Spatially-explicit (6-32 m^2)	NA	1 month	Lizard Island	Cover of 14 hard corals + 3 soft corals	Growth (lateral expansion); mortality (total + partial); recruitment; competition	Cyclones; bleaching; CoTS	Compete©
CotSim Scandol 1993, 1999, Fabricius et al. 2010	Computational	Applied; predictive	Population-based (but CoTS-centric); stochastic	Simulate spatial distribution of CoTS on the GBR and effects on corals	Spatially-structured (reef)	CoTS connectivity (Dight et al 1990, James et al. 2002)	1 yr	GBR	Cover of 2 coral groups (fast + slow growing), density of CoTS (8 age classes)	Population growth (logistic) + impacts of CoTS	CoTS	Software? R (Fabricius et al. 2010)
Model of CoTS-corals II Morello et al. 2014	Computational	Applied; predictive	Population-based (but CoTS-centric); deterministic	Evaluate the impact of predation and management control on CoTS	NA	NA	1 yr	Arbitrary or calibrated (Lizard Island)	Cover of 2 coral groups (fast + slow growing), density of CoTS (3 age classes)	Population growth (logistic) + impacts of CoTS	CoTS	AD Model Builder
Model of CoTS-corals III Mellin et al. 2016	Computational	Applied; predictive	Population-based; stochastic	Forecasting CoTS invasions under climate change	Spatially-explicit 1-10,000 km2	Random dispersion	1 yr	Empirical (CoTS, corals) or arbitrary (habitat suitability, climate change)	Coral abundance (or cover?), CoTS abundance	Population growth (linear) + consumption by CoTS	Abstract impact of climate change (affects carrying capacity)	Python
Empirical (logistic) model of coral recovery Mumby & Anthony 2015, Wolff et al. 2016, 2018	Analytical	Applied; predictive	Population-based (Acropora); deterministic (but stochastic disturbances)	Explore scenarios of coral persistence	Spatially-structured (reef)	NA	1 yr	GBR	Acropora cover	Population growth (logistic) + impacts of disturbances	CoTS, bleaching, cyclones, nutrients, OA	NA
Empirical (Gompertz) model of coral recovery Osborne et al. 2017	Analytical	Applied; predictive	Population-based (Acropora and other corals); probabilistic	Assess recovery rate of coral cover	NA	NA	1 yr	GBR	Cover of Acroporidae and other corals	Population gorwth (Gompertz)	NA	NA
HOME McCook et al. 2001, Wolanski et al. 2004	Analytical	Applied; predictive	Population-based; deterministic	Predict coral/algal cover	Spatially-structured (reef)	Coral connectivity (Thomas et al. 2014)	0.01 yr	Arbitrary or empirical (?)	Cover of juvenile + adult corals, cover of algae, herbivorous fish	Population growth (logistic) + recruitment + mortality + maturation	Cyclones, river plume (sediments, nutrients)	NA
Model of coral-algal interactions II Mumby et al. 2007, Anthony et al. 2011	Analytical	Applied; predictive	Population-based; deterministic	Explore scenarios of coral persistence	NA	NA	1 yr	Empirical/absract	Coral and maroalgal cover	Population growth + mortality + competition with algae + herbivory	Cyclones, bleaching, OA, fishing	NA
Model of coral-algal interactions III van den Leemput et al. 2016, Hughes et al. 2017	Analytical	Theoretical; descriptive	Population-based; deterministic	Explore scenarios of coral persistence	NA	NA	Abstraction	Abstraction	Coral and macroalgal cover	Population growth + recruitment + mortality + competition with algae + herbivory	fishing (herbivores), climate change (corals) and pollution (algae)	NA
Model of carbon flux Johnson et al. 1995	Flow model	Applied; descriptive	Trophic compartments	Explore effects of community shift on trophic functioning (pathways of carbon flux)	NA	NA	Static	Davies Reef + GBR midshelf reef	Input and output carbon flows for each compartment	Photosynthesis, respiration, carbon translocation to host, loss due to predation by corallivores.	NA	NA
Model of coral polyp in eReefs Baird et al. 2013; Gustafsson et al. 2013; Mongin and Baird 2014	Computational	Applied; predictive	Physiological	Predict the local productivity of GBR corals over continuous time	Spatially-realistic (GIS layers)	Hydrodynamic and biogeochemical environment at depth across the GBR (1km and 4km resolution)	1 d	Empirical and comprehensive (physical and biogeochemical)	Coral tissue biomass, zooxanthella biomass and rates of calcification and carbonate calcium dissolution at depth	Physiological (tissue) growth and mortality	Physiological response to fluctuations in physical and biogeochemical environment (light, temperature, nutrients, particulate organic matter, aragonite saturation)	GIS layers
Model of coral energy budget Anthony & Connolly 2004, Anthony et al. 2009	Dynamic energy budget	Applied; predictive	Physiological	Predict coral mortality after bleaching	NA	NA	1 d	Empirical (experiments on Acropora)	Chlorophyll, energy budget, energy stores	Physiological processes (photosynthesis, respiration heterotrophy, excretion)	Physiological response to fluctuations in light, temperature and turbidity	NA