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CoCoNet

Coral Community Network Model

User Guide
&
Technical Summary

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Scott A. Condie

Javier Porobic

Reef Restoration and Adaptation Program, a partnership:

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Acknowledgments

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1 User Guide

1.1 Purpose of the CoCoNet model

The Coral Community Network (CoCoNet) model was developed to explore the role of physical and ecological processes in controlling the health of coral reef systems in the past and future. This includes understanding reef futures under different climate scenarios and options for interventions aimed at protecting and restoring coral reefs. However, it should be recognised that coral reefs are some of most complex ecosystems on Earth and models can only provide a highly simplified representation of the real system. The purpose of CoCoNet is therefore to capture the most important components and processes controlling the long-term trajectory of the system.

The CoCoNet modelling system has been developed to meet a range of functional and non-functional requirements (Appendix A), with a view to meeting the long-term needs of the broader coral reef modelling community. This includes a focus on maintainable code and high computational efficiency able to support large ensemble runs and rigorous estimation of model uncertainty.

The current version of CoCoNet has been implemented and calibrated for the Great Barrier Reef (GBR) system, where it is used to test a diverse range of interventions.

1.2 CoCoNet modelling environment

The Coral Community Network (CoCoNet) model has been developed within the NetLogo environment (v. 6.0.4). NetLogo is an agent based programmable modelling environment (https://ccl.northwestern.edu/netlogo/) used widely across many science disciplines. All models developed within NetLogo are packaged within a single file with tabs for a user interface, model documentation, and model code.

1.3 Installing and running CoCoNet

(i) Install Netlogo free of charge at https://ccl.northwestern.edu/netlogo/6.0.4/

(ii) Upload the CoCoNet model, the coastline file and the reef file (Table 1).

(iii) Open CoCoNet and select the interface tab.

(iv) Specify run parameters within the interface:

- parameter filename: if file is in the local directory, then all parameters will be taken from this file and interface parameters will be ignored.
- output filename
- climate scenario
- size of ensemble

- run period
- intervention parameters

(v) Click on the "setup" button.

(vi) Click on the "go" button to run the ensemble of runs.

The files required to run CoCoNet are listed in Table 1 and all output variables recorded in the standard output file (annually at every reef) are listed in Table 2.

Table 1 List of files required to run the CoCoNet model and the standard output file. Note that if the parameter file name specified in the interface is not in the local directory, then parameters are taken instead from the interface.

Status	Description	Current filename	File type
Essential	CoCoNet model code and user interface.	CoCoNet V3 Feb2023.nlogo	Netlogo (.nlogo)
	Coastline definition containing a list of longitudes and latitudes.	coastline.csv	Comma separated values (.csv)
	List of all reefs and their key properties (e.g. name, longitude, latitude, size, geographical sector, zoning).	Reefs2024.csv	Comma separated values (.csv)
Optional	List of model parameter values (defaults to interface value if this file is not in the local directory).	parameters#.csv	Comma separated values (.csv)
Generated during runtime	CoCoNet output file generated during runtime (content as listed in Table 2).	Specified in the user interface	Comma separated values (.csv)

Table 2 Variables generated by CoCoNet for every reef on an annual timestep.

Reef variable	Definition	Typical values or range
Ensemble	Run ensemble number	[1 50]
Year	Year	YYYY
Reef_ID	Reef ID number	xx-xxx
Region_name	S=south, C=central, N=north, FN= far-north	S, C, N or FN
Shelf_position	I=inner-shelf, M=mid-shelf, O=outer-shelf	I, M or O
Rezone_year	Year that zoning changes from blue (fishing allowed) to green (fishing excluded)	YYYY
Priority	Priority for control of CoTS (N=non-priority, P=priority, T=target)	N, P, T
Longitude	Longitude of reef	[142.19 153.15]
Latitude	Latitude of reef	[-24.64 -10.35]
km_offshore	Distance offshore in kilometres	[0 300]
Reef_sites	Number of standard CoTS control sites (~ 10 ha of coral habitat) on reef	[1 1724]
C_sa	Coral cover – staghorn *Acropora* species	[0 1]
C_ta	Coral cover – tabular *Acropora* species	[0 1]
C_mo	Coral cover – *Montipora* species	[0 1]
C_po	Coral cover – *Poritidae* species	[0 1]
C_fa	Coral cover – *Favids* species	[0 1]
C_tt	Coral cover – thermally tolerant species (intervention)	[0 1]
C_out_degree	Weighted out-degree (recruits dispersed to other reefs)	[0 20]
Rubble	Rubble cover	[0 1]
DHW	Degree heating weeks	[0 100]
bleach_sa	Bleaching mortality – staghorn *Acropora* species	[0 1]

Reef variable	Definition	Typical values or range
bleach_ta	Bleaching mortality – tabular *Acropora* species	[0 1]
bleach_mo	Bleaching mortality – *Montipora* species	[0 1]
bleach_po	Bleaching mortality – *Poritidae* species	[0 1]
bleach_fa	Bleaching mortality – *Favids* species	[0 1]
bleach_tt	Bleaching mortality – thermally tolerant species	[0 1]
Maximum_cyclone_category	Highest cyclone category in year	[1 5]
cyclone_sa	Cyclone mortality – staghorn *Acropora* species	[0 1]
cyclone_ta	Cyclone mortality – tabular *Acropora* species	[0 1]
cyclone_mo	Cyclone mortality – *Montipora* species	[0 1]
cyclone_po	Cyclone mortality – *Poritidae* species	[0 1]
cyclone_fa	Cyclone mortality – *Favids* species	[0 1]
cyclone_tt	Cyclone mortality – thermally tolerant species	[0 1]
predate_sa	CoTS predation mortality – staghorn *Acropora* species	[0 1]
predate_ta	CoTS predation mortality – tabular *Acropora* species	[0 1]
predate_mo	CoTS predation mortality – *Montipora* species	[0 1]
predate_po	CoTS predation mortality – *Poritidae* species	[0 1]
predate_fa	CoTS predation mortality – *Favids* species	[0 1]
predate_tt	CoTS predation mortality – thermally tolerant species	[0 1]
S_1	Starfish per hectare - juveniles	Not recorded
S_2	Starfish per hectare – age 2 years	< 100
S_3	Starfish per hectare – age 3 years	< 100
S_4	Starfish per hectare – age 4 years	< 100
S_5	Starfish per hectare – age 5 years	< 100
S_6	Starfish per hectare – age 6+ years	< 100
Control_dives	Control dives on reef	< 50
Benthic_invert	Benthic invertebrates (preying on juvenile CoTS) per hectare	< 10,000
Triggerfish	Triggerfish per hectare	< 200
E_1	Emperor fish per hectare – juveniles	< 100
E_2	Emperor fish per hectare – age 2 years	< 100
E_3	Emperor fish per hectare – age 3 years	< 100
E_4	Emperor fish per hectare – age 4 years	< 100
E_5	Emperor fish per hectare – age 5 years	< 100
E_catch_kg	Emperor fish catch – age 3-5 years	< 2000
G_1	Grouper fish per hectare – juveniles	< 200
G_2	Grouper fish per hectare – age 2 years	< 200
G_3	Grouper fish per hectare – age 3 years	< 200
G_4	Grouper fish per hectare – age 4 years	< 200
G_5	Grouper fish per hectare – age 5 years	< 200
G_catch_kg	Grouper fish catch – age 3-5 years	< 5000

CoCoNet is defined by the equations, variables and parameter values described in the Technical Summary (Section 2). Parameters relating to the calibrated GBR implementation are specified within the model code and need only be changed if an expert user wishes to improve the existing calibration or implement new types of interventions (Figure 1). The user interface allows any user to specify a climate scenario; the length of model run; the number of runs within the model ensemble; and a wide range of intervention options (Figure 2). All options are defined in Tables 3 and 4.

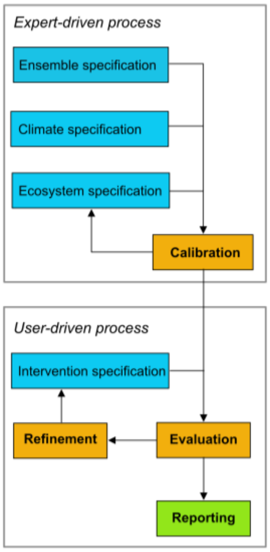

Figure 1: CoCoNet modelling system specification categorised by expert-driven processes and user-driven processes.

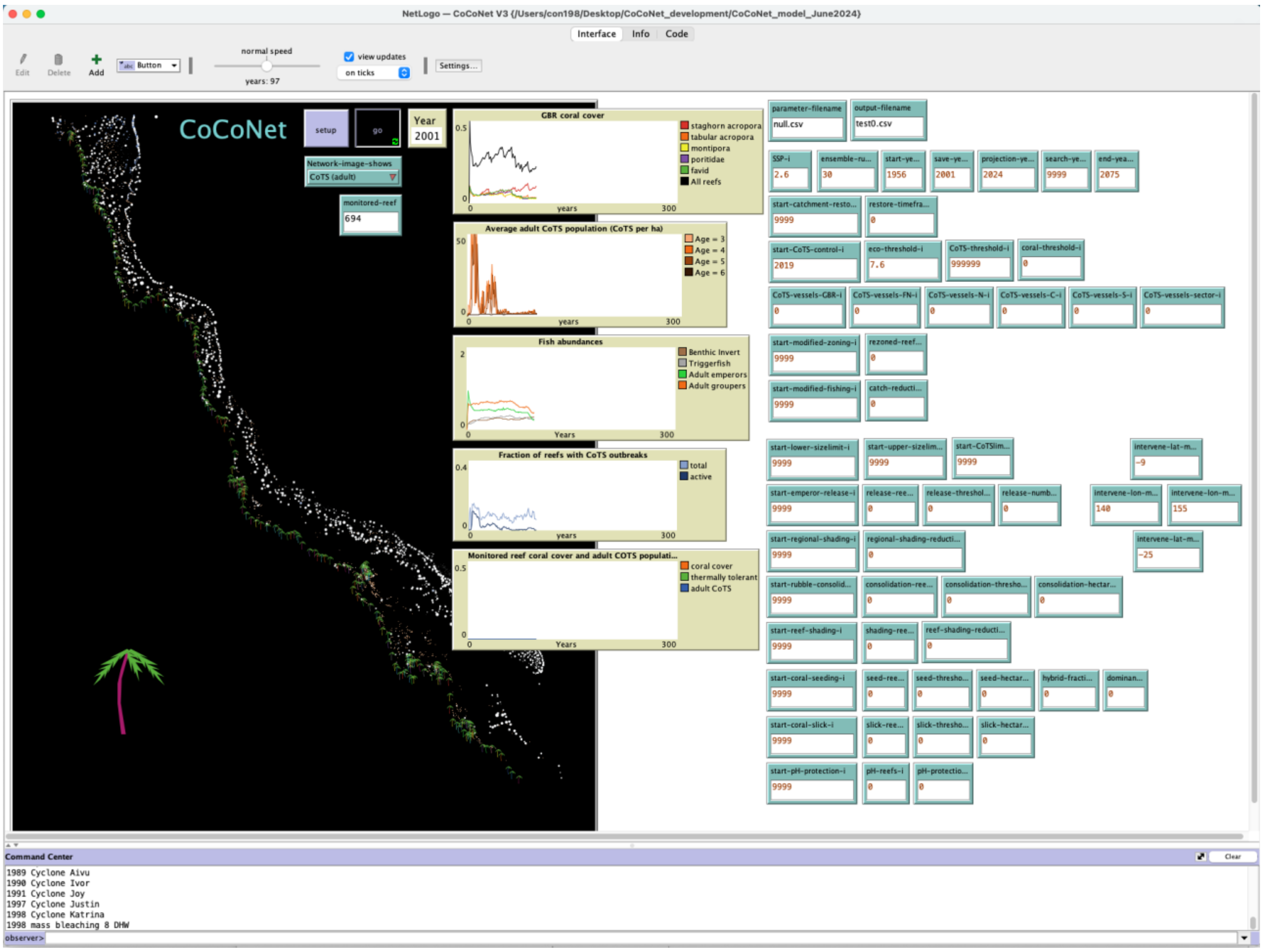

Figure 2: User interface used to specify model conditions and show spatial and time-series outputs during runtime. Note that "view updates" should usually be unselected, otherwise annual updating of the map will dramatically increase model runtime.

Table 3 Definition of parameters specified in the parameter file (if in local directory) or the CoCoNet interface relating to run conditions and broadscale intervention options.

Category	Parameter	Definition
Run conditions	parameter-filename	File containing parameters defining the run and interventions. If the file is not in the local directory, then the model will instead use parameters specified in the interface.
	output-filename	Output file specifying run and conditions on all reefs from year 'save-year' to year 'end-year'.
	SSP	The CMIP6 client scenario (1.9=SSP1-1.9, 2.6=SSP1-2.6, 4.5=SSP2-4.5, 7.0=SSP3-7.0, 8.5=SSP5-8.5).
	ensemble-runs	Number of runs in ensemble used to capture model uncertainty.
	start-year	First year of each model run (note that first run includes the prior 50-years for equilibration).
	save-year	Year from which model outputs are saved to 'output-filename'.
	projection-year	Year from which historical forcing is replaced by stochastic projections.
	search-year	Year from which benefit of intervention at a single reef is tested to find best performing reefs.
	end-year	Final year of each model run.
CoTS control	start-CoTS-control	Year from which CoTS control program begins.
	eco-threshold	Minimum density of CoTS on a site for deployment of CoTS control (CoTS per ha).
	CoTS-threshold	Maximum density of CoTS on a reef for deployment of CoTS control (CoTS per ha).
	coral-threshold	Minimum coral cover on a reef to over-ride CoTS-threshold.
	CoTS-vessels-GBR	Number of control vessels operating across the GBR.
	CoTS-vessels-FN	Number of control vessels operating in the Far North region.
	CoTS-vessels-N	Number of control vessels operating in the North region.
	CoTS-vessels-C	Number of control vessels operating in the Central region.
	CoTS-vessels-S	Number of control vessels operating in the South region.
Catchment restoration	start-catchment-restore	Year from which catchment restoration program begins.
	restore-timeframe	Time for restoration of catchments (years).
Fisheries zoning	start-modified-zoning	Year from which new zoning of reefs begins (blue to green).
	rezoned-reefs	Number of reefs rezoned from Blue (fishing permitted) to Green (fishing not permitted).
Fishing rates	start-modified-fishing	Year from which new fishing rates begin.
	catch-reduction	Fractional reduction in fishing rates [0 1].

Table 4 Definition of parameters specified in the CoCoNet user interface relating to local or regional interventions.

Category	Parameter	Definition
Region for interventions below	intervene-lat-min	Minimum latitude of regional interventions below (e.g. -17).
	intervene-lat-max	Maximum latitude of regional interventions below (e.g. -16).
	intervene-lon-min	Minimum longitude of regional interventions below (e.g. 146).
	intervene-lon-max	Maximum longitude of regional interventions below (e.g. 147).
Limits on fishing	start-CoTSlimit	Year from which to exclude fishing from reefs with active outbreaks of CoTS (> 68 per ha).
	start-lower-sizelimit	Year from which to impose restrict catches to fish > 3-years old.
	start-upper-sizelimit	Year from which to impose restrict catches to fish < 5-years old.
Regional-shading	start-regional-shading	Year from which large-scale solar radiation management begins.
	shading-dhw	Reduction in heating associated with solar radiation management (DHW)
Coral rubble consolidation	start-rubble-consolidation	Year from which rubble consolidation program begins.
	consolidation-reefs	Number of reefs consolidated.
	consolidation-threshold	Minimum rubble cover threshold for deployment of consolidation on a reef [0 1].
	consolidation-hectares	Total annual consolidation capacity (hectares of rubble).
Local reef shading	start-reef-shading	Year from which individual reef shading program begins.
	shading-reefs	Number of reefs shaded.
	shading-fraction	Fraction of reef shaded.
Thermally tolerant coral seeding	start-coral-seeding	Year from which coral seeding program begins.
	seed-reefs	Number of reefs seeded.
	seed-threshold	Maximum coral cover threshold for deployment of seeding on a reef [0 1].
	seed-hectares	Total annual seeding capacity (hectares).
	hybrid-fraction	Fraction of staghorn acropora capable of hybridising with thermally tolerant corals [0 1].
	dominance	Dominance of thermal tolerance trait during hybridisation [0 1].
Coral larval slick deployment	start-coral-slick	Year from which coral slick program begins.
	slick-reefs	Number of reefs where coral slicks are deployed.
	slick-threshold	Maximum coral cover threshold for deployment of coral slicks on a reef [0 1].
	slick-hectares	Total annual coral slick capacity (hectares).
Local pH buffering to reduce OA effects	start-pH-protection	Year from which pH protection begins.
	pH-reefs	Number of reefs where pH treatments are deployed.
	pH-protection	Fractional level of protection from OA effects [0 1].

2 Technical summary

The Coral Community Network (CoCoNet) model is a meta-community model that includes communities of corals, crown-of-thorns starfish (CoTS, preying on corals), benthic invertebrates (that prey on juvenile CoTS), and key fish groups including invertivores (e.g. triggerfish, preying on benthic invertebrates), emperors (e.g. red-throat and spangled emperors, preying on juvenile and adult CoTS) and groupers (e.g. coral trout, preying on invertivore fish) (Figure 3). The population age-structures of CoTS, emperors and groupers are explicitly represented. Populations of all groups are distributed across a network of 3806 reefs, each resolved at a site-scale encompassing ~10 ha of coral habitat, which also equates to the coverage of individual dives undertaken by the CoTS control program.

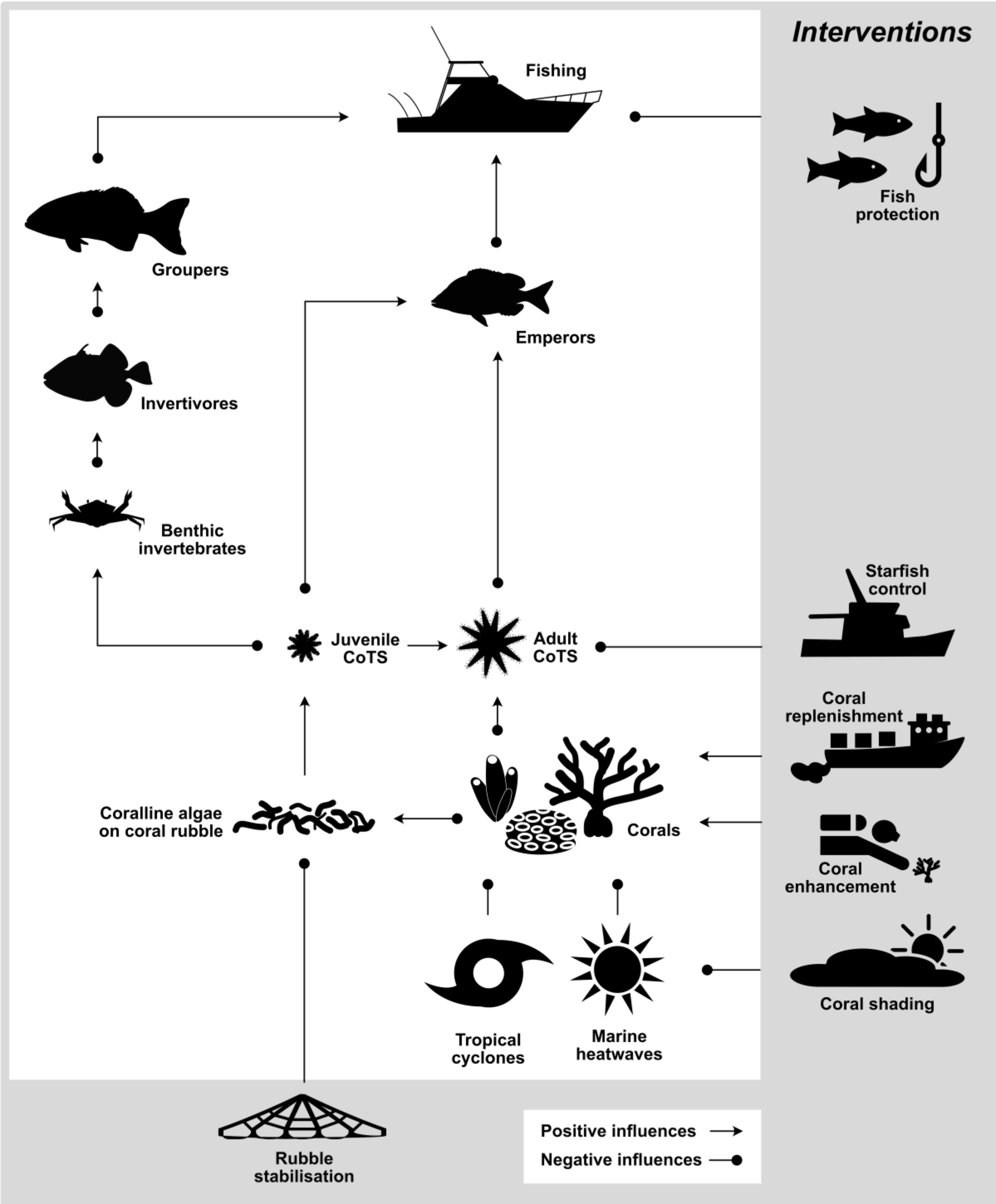

Figure 3: Food web structure within the CoCoNet model, plus influences from environmental extremes (tropical cyclones, marine heatwaves), human impacts (fishing), and human intervention strategies (fish protection including zoning, CoTS control, coral replenishment, coral enhancement, coral shading and rubble stabilisation). Arrows indicate a positive effect and circles a negative effect. model. Corals consist of 5 functional groups, while the populations of CoTS, groupers and emperors are each age-structured.

The key processes represented in CoCoNet are described in more detail below, but can be very briefly summarised as follows:

- At every site of every reef, populations of corals, CoTS, benthic invertebrates and fish are tracked as they grow, compete, reproduce, and interact through predator-prey dynamics.
- Reproduction involves recruitment at site-scale, reef-scale, or inter-reef scale, where inter-reef recruitment is determined by larval dispersal based on modelled ocean currents.
- Corals can only recruit to bare substrate, whereas CoTS can only recruit to coral rubble (generated by coral mortality).
- Tropical cyclones and marine heatwaves are applied following historical patterns and then according to probability distributions based on future climate projections.
- Coral mortality is dependent on the strength and spatial coverage of each cyclone or heatwave event, with the latter driving natural selection for more thermally tolerant corals.
- Ocean acidification influences future growth rates of corals and their susceptibility to cyclone damage.

Many aspects of the CoCoNet model and its application have also been described in previous publications (Table 5).

Table 5 Previous publications describing implementation and applications of CoCoNet.

Version	Title of publication	Reference
1.0	Great Barrier Reef recovery through multiple interventions	(Condie et al. 2018)
2.0	Large-scale interventions may delay decline of the Great Barrier Reef	(Condie et al. 2021)
2.0	Assessing changes to ecosystem service values at large geographic scale: A case study for Australia's Great Barrier Reef	(Stoeckl et al. 2021)
2.0	Changing the climate risk trajectory for coral reefs	(Condie 2022)
2.0	Control efforts of crown-of-thorns starfish outbreaks to limit future coral decline across the Great Barrier Reef	(Castro-Sanguino et al. 2023)

2.1 Environmental forcing

Reefs were exposed to environmental forcing in the forms of ocean currents (reef connectivity through larval dispersal), tropical cyclones (physical damage of corals), flood plumes (restricted growth of corals), and heatwaves (coral bleaching and mortality). While flood plumes are often assumed to enhance the survival of CoTS larvae by increasing the availability of planktonic food (Fabricius et al. 2010), recent evidence points to the negative effects of lower-salinity water on CoTS larvae (Clements et al. 2022). Hence, within CoCoNet, the net effect of flood plumes on CoTS has been assumed to be small.

For the historical period (1961-2021) environmental forcing was based on observed cyclones and marine heatwave events, whereas future environmental forcing (2022-2100) has been estimated from climate projections. In the absence of any clear trend in tropical cyclone patterns (Knutson et al. 2020), it was assumed that future statistical distributions of cyclone frequency and intensity would be similar to the recent past.

The frequency and intensity of marine heat waves were assumed to increase within probability distributions derived by semi-dynamically downscaling surface-level atmospheric data from a multi-model ensemble of five CMIP6 models (MRI-ESM2-0, EC-Earth3-Veg, UKESM1-0-LL, CNRM-ESM2-1, and IPSL-ESM2-0) that adequately span the range of CMIP6 model responses (McWhorter et al. 2022). Results from this ensemble of climate models were used to derive trajectories (2023-2100) for the probability of a marine heatwave in any year and the magnitude distribution of associated heat stresses (McWhorter et al. 2022). These quantities were available for five Shared Socioeconomic Pathways: SSP1-1.9, SSP1-2.6, SSP2-4.5, SSP3-7.0, and SSP5-8.5 (four are shown in Figure 4) that were each used to generate an ensemble of stochastic time-series for maximum degree heating weeks (DHW_{max}) for 2023-2100. The spatial distribution of DHW within any year could then be approximated by a linear decay centred around a randomly selected reef allocated DHW_{max} for that ensemble member and year.

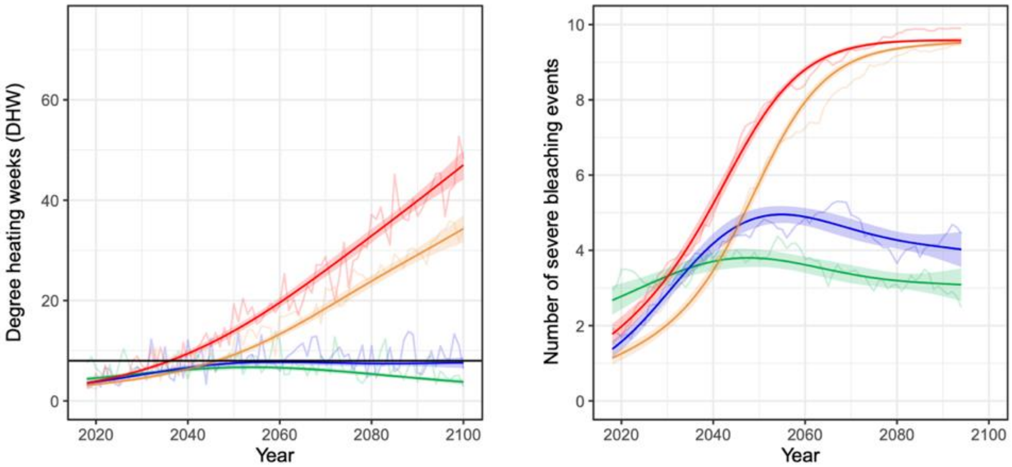

Figure 4 Heat stress averaged across the Great Barrier Reef for four socioeconomic pathways (SSP1-1.9, SSP1-2.8, SSP3-7.0, SSP5-8.5) derived from an ensemble of five climate models (MRI- ESM2-0, EC-Earth3-Veg, UKESM1-0-LL, CNRM-ESM2-1 and IPSL-ESM2-0). The magnitude of heating events in units of DHW (left) and the probability of a severe bleaching event in units of average events per decade (right). The curves are smoothed Generalised Additive Models (GAMs) fitted to the data, with shaded areas denoting the standard deviation for each scenario averaged across models (McWhorter et al. 2022). Heat stress above the horizontal black line (8 DHW) is likely to result in severe bleaching and coral mortality.

2.2 Larval dispersal and reef connectivity

For all coral groups, larval production was proportional to their areal coverage. CoTS larval production was proportional to the number of adult starfish and also increased by a factor of 4 for each age class (Babcock et al. 2016) before plateauing after age 4 years (Lucas 1984, Pratchett et al. 2014). Emperor and grouper larval production per individual doubled for each age-class (Barneche et al. 2018). However, it also decreased towards the equator by approximately 40%, due to sensitivity of fish larvae to high ocean temperatures (Pratchett et al. 2017b). Allee effects also limited fertilisation rates of both coral (Mumby et al. 2024) (Figure 4.x) and CoTS (Rogers et al. 2017).

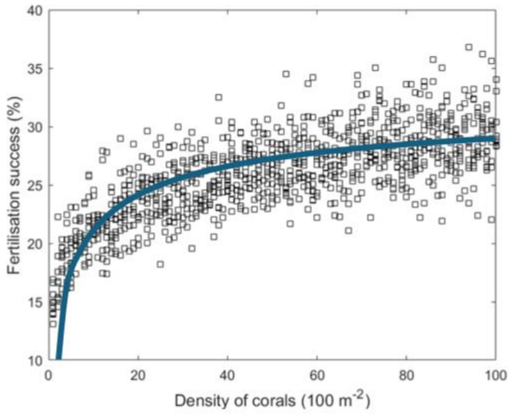

Figure 4.x: Palau data (Mumby et al. 2024) indicated by hollow squares compared with CoCoNet parameterisation of coral fertilisation assuming maximum fertilisation success is 35%.

Parameterisation of reef connectivity needed to capture the processes of spawning, larval transport by ocean currents and successful settlement onto either the natal reef or neighbouring reefs (Table 6). Dispersal following spawning at each reef was modelled using particle tracking techniques based on the OceanParcels code (https://oceanparcels.org). The underlying ocean currents were provided by 7-years of simulation (2015-2022) using the eReefs 1 km resolution hydrodynamic model (Condie and Condie 2016, Hock et al. 2019, Steven et al. 2019, Baird et al. 2021). Particles were released from all reefs over the relevant spawning periods and then tracked as they were advected by the current fields at the preferred swimming depths of larvae (Table 6).

Table 6 Fields and parameters required to estimate coral connectivity for use in the CoCoNet model.

Processing stage	Fields and parameters	Coral	CoTS	Groupers	Comments
1. Currents & winds	Local currents	RECOM (~200m)			Estimate potential for retention on reefs with particular characteristics (size, depth, tidal range).
	Regional currents	eReefs GBR1 (1km)			Latest version (GBR1:H2.0)
	Winds	GBR1 forcing			Latest version (GBR1:H2.0)
2. Particle trajectories	Release polygons	Reef polygons + convex hulls			Not yet updated to high-resolution habitat maps (e.g. Allen Coral Atlas).
	Spawning years	2015/16 – 2021/22			eReefs currents available.
	Spawning months	Oct, Nov, Dec	Dec, Jan	Dec, Jan	Coral spawning weighted by location. CoTS spawning continuous (Caballes et al. 2021)
	Spawning times	8pm – 12pm, 3, 4, 5 and 6 nights after full moon	Continuous	Continuous	Particles: 5-hours x 100 per hour = 500 per day per reef (C. Doropoulos and dispersal analysis).
	Larval depth trajectory	0.0 - 0.5 days @ 0m 0.5 - 2.5 days @ 2m 2.5 - 28 days @ 5m			Using 2-D currents with depth at age preferred to 3-D currents with sinking at age due to potential for unrealistic vertical distributions.
	Maximum age of larval settlement competency	35 d	45 d	35 d	Maximum time that particles are tracked (Frisch et al. 2016).
3. Connectivity matrices	Settlement polygons	Reef polygons + convex hulls + capture halo			Halo allows for unresolved flow features and weak swimming of larvae towards reefs (Hata et al. 2017).
	Minimum age of larval	3.3 d			Particles are not removed at reefs and settlement probabilities are scaled (Moneghetti et al. 2019)

Processing stage	Fields and parameters	Coral	CoTS	Groupers	Comments
	settlement competency				
	Mortality timescale	Acropora: 38 d Merulinids: 12 d			(Connolly and Baird 2010, Moneghetti et al. 2019).
	Weight of spawnings	Oct: inshore 70%; offshore 0% Nov: inshore 30%; offshore 30% Dec: inshore 0%; offshore 70%			Under review.

Particles passing within 1 km of a reef were counted as potentially contributing to recruitment at that reef. The 1 km halo took into consideration errors in the current fields near reefs (1 km resolution) and any swimming ability of larvae (fairly negligible for corals and CoTS). The time that a particle had spent reaching that reef was also taken into account in terms of the larval mortality rate, the minimal age that larvae are competent to settle, and the maximum age that larvae are competent to settle.

The probability of spawning at one reef contributing to recruitment at another reef was described in terms of a spatial dispersal kernel (Kaplan 2006, Aiken et al. 2007). For each functional group and spawning period, a kernel was calculated for every reef, consisting of 2 sectors enclosing > 80% of downstream reefs. Each sector was defined by a minimum radius, a maximum radius, a direction (degrees clockwise from north), and an arc radius (degrees). This allowed downstream kernels for any functional group, spawning period and recruiting reef to be efficiently computed and specified within the model. Kernels from the same year were always applied across all functional groups to ensure consistent dispersal patterns. However, the year was chosen randomly from the 6 available years (except for the 7 years directly matching eReefs).

The probability of larval recruitment was also proportional to the availability of suitable habitat on receiving reefs. For coral, this corresponded to the proportion of area without existing coral or rubble cover; for CoTS, it only included the proportion of area with rubble cover; and for reef fish, it included the entire reef area. Hence coral rubble generated previously by cyclones or bleaching mortality reduced the settlement of coral and increased the settlement of CoTS.

Local retention was estimated using data from particle tracks generated by using high resolution models of individual reefs (RECOM) nested inside GBR1. Particles released on a reef were considered retained while ever they remained inside the 20 m depth contour. The fraction of particles retained was then tracked over time.

Results from 25 reefs suggest that the fraction of particles retained on any reef decays exponentially over a number of days:

$$\tau = a\sqrt{S} \tag{1}$$

where S is the number of control sites and $a = [0.04\ 0.22]$, in units of days per root number of sites, spans all 25 modelled reefs (Figure 5). Given that retention times tend to increase with the resolution of the underlying flow fields (Saint-Amand et al. 2023a, Saint-Amand et al. 2023b), the approach is likely to underestimate retention times. We have therefore adopted a value of $a = 0.2$ days sites$^{-0.5}$, near the upper end of the range (Figure 5).

For CoTS, if we also assume settlement starts at $t_{settle} = 10$ days (Pratchett et al. 2017a), then the retention is

$$R = e^{-t_{settle}/\tau} = e^{-50/\sqrt{S}} \qquad (2)$$

Hence, a reef like John Brewer with 59 sites can retain up to 0.01%, whereas a very large reef like Corbett with 601 sites can retain up to 6%.

For corals, if we also assume settlement starts at $t_{settle} = 4$ days (Moneghetti et al. 2019), then the retention is

$$R = e^{-t_{settle}/\tau} = e^{-20/\sqrt{S}} \qquad (3)$$

Hence, a reef like John Brewer with 59 sites can retain up to 7%, whereas a very large reef like Corbett with 601 sites can retain up to 44%.

For groupers, settlement starts at 25 days (Frisch et al. 2016). However, they develop significant swimming ability before that time that may assist with retention. It has therefore been assumed that $t_{settle} = 10$ days for groupers. Reef larval retention is not relevant to emperors, which mature on remote seagrass nursery beds. Instead, they are assumed to recruit exclusively to reefs within 50 km of their natal reef.

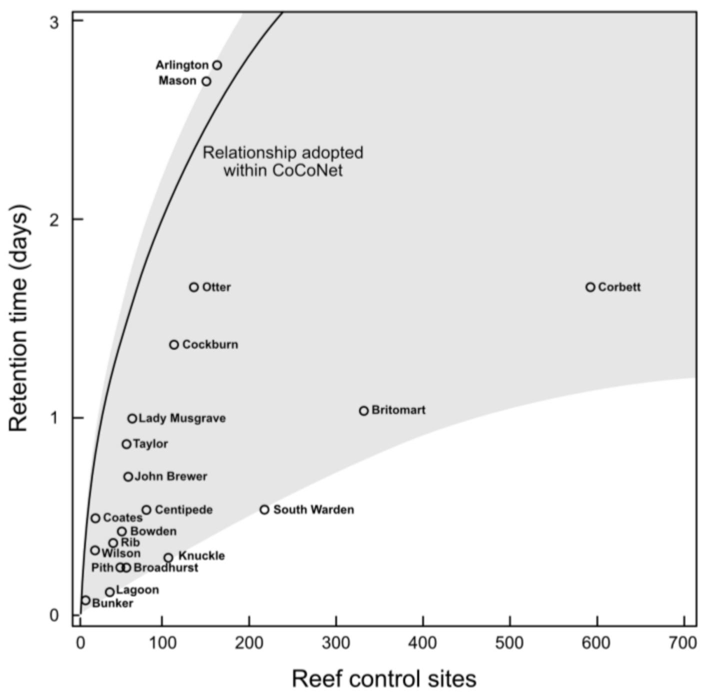

Figure 5: Graph of retention time (days) verses number of control sites on the reef (proportional to coral habitat area). The grey area encapsulates results from all 25 reefs and the black curve indicates the relationship adopted within CoCoNet. For each reef, the rate of particle loss was modelled using RECOM and this data used to estimate a retention time by fitting an exponential decay curve (provided by Dr Jim Greenwood, CSIRO).

2.3 Ecological interactions and responses

Ecological communities represented on each reef included corals, CoTS, benthic invertebrates, planktivorous fish, invertivorous fish, and emperor and grouper fish groups (Table 7). Each reef had a fixed coral-carrying capacity proportional to the area of coral habitat on the reef. Every reef was resolved at the spatial scale of a CoTS control site, which on average corresponds to ~10 ha of coral habitat, or the area sampled by 544 manta tows from the Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP).

Coral communities consisted of five coral groups whose species are relatively abundant on the GBR (DeVantier and Turak 2017). These groups nominally corresponded to staghorn Acropora, tabular Acropora, Montipora, Poritidae and favids, distinguished within the model in terms of their growth rates, preference by CoTS, and susceptibility to environmental impacts such as cyclones and marine heatwaves (Appendix A). Differences in fecundity among coral groups were assumed to be independent of geographical location along the GBR (Tan et al. 2016) and negligible compared with differences in environmental susceptibility (Alvarez-Noriega et al. 2016).

CoTS populations were size-structured, differentiating larvae (age 0 years), herbivorous juveniles (age 1 year) and four corallivorous adult classes (ages 2, 3, 4 and 5+ years). A proportion of juveniles could delay their transition to adult stage if the cover of their preferred coral was low (Deaker et al. 2020). Trophic interactions between corals and CoTS were calculated using a formulation that included doubling of adult CoTS predation rates until age 4 (Frieler et al. 2013) when they began to move into a senescent phase (Pratchett et al. 2014). CoTS preferred for faster-growing corals (Pratchett 2010) and populations declined when these became rare.

Additional groups have been included in CoCoNet specifically to model the effects of direct and indirect predation on CoTS and how these predation levels are reduced by fishing. Key groups include benthic invertebrates, invertivores (triggerfish and cardinal fish), emperors (red-throated and spangled) and groupers (coral trout species). Trophic interactions between these groups are indicated in Figure 3 and Table 7, with detailed equations and parameter values listed in Appendix A. Only the main trophic links indicated by available empirical data have been included (Cowan et al. 2017, Kroon et al. 2020, Kroon et al. 2021), with less frequent predation assumed to have only a minor influence on the trajectory of the system (e.g. direct predation on CoTS by fish invertivores, Figure 3). Predation rates of age-structured fish (emperors and groupers) were assumed to increase linearly with age.

For each ecological group in the model, rate parameters such as growth, predation and natural mortalities were either based directly on available empirical data or fitted to LTMP data (Table A.5) (Morello et al. 2014, Plaganyi et al. 2014, Condie et al. 2021).

Table 7 Groups included in the CoCoNet model with their ecological characteristics and monitoring status.

Group	Symbol	Age-structure (years)	Adult movement range	Laval recruitment range	Predate on	GBR monitoring
Benthic invertebrates (decorator crabs, others)	B	N/A	Site	Natal site only	Juvenile CoTS	Nil
CoTS	S	0,1,2,3,4,5,6+	Site	Natal and remote reefs	Coral	LTMP
Corals (5 groups)	C	N/A	Site	Natal and remote reefs	Larval CoTS	LTMP
Invertivores (triggerfish, cardinal fish)	T	N/A	Site	Natal reef	Benthic invertebrates	Nil
Emperors (red-throated *Lethrinus miniatus* and spangled *Lethrinus nebulosus*)	E	0,1,2,3,4,5+	Reef	Natal and remote reefs	Juvenile & adult CoTS	LTMP (some species)

Groupers (7 coral trout species, predominately *Plectropomus leopardus*)	G	0,1,2,3,4,5+	Reef	Natal and remote reefs	Damselfish & triggerfish	LTMP (some species)

2.4 Fisheries

Commercial and recreational catches recorded from 1989 to 2021 were used to estimate emperor and grouper catch probability distributions as a function of offshore distance, latitude and year. These probability distributions were approximated by analytical functions in the model that extrapolated both backwards in time (increasing over the period 1940-1988 assuming up to 50% unreported) and forward in time (mean catch fixed from 2022). Catch rates were assumed to be zero for fish under 3-years of age and equal for all ages from 3-years.

While less precise than utilising raw catch data, this approach is consistent other probabilistic aspects of the model supporting the ensemble modelling approach (e.g. incidences of tropical cyclones and heatwaves, and specification of connectivity in terms of dispersal kernels) and ensures that no confidential fisheries data can be accessed via the model.

Zoning regulations were applied in the model from 1987 when 171 reefs were declared as Green Zones excluding fishing, expanding to 1269 reefs in 2004. It was assumed that all fishing (reported and unreported) occurred within the remaining Blue Zones, where fishing was permitted.

2.5 Model calibration

CoCoNet has been calibrated against the LTMP dataset (Sweatman et al. 2011) at both the individual reef scale (Morello et al. 2014, Plaganyi et al. 2014) and reef network scale (Condie et al. 2018, Condie et al. 2021). It has successfully reproduced historical trajectories of regional coral cover and CoTS outbreak densities, as well as emergent system responses such as CoTS outbreaks and coral recovery at close to their observed periodicity (Condie et al. 2018).

Comparisons of CoCoNet results with LTMP data at GBR scale confirm that trends in coral cover, emperor density, grouper density, CoTS density, CoTS outbreak rate, and reefs controlled, are broadly consistent (Figures 6-8), as are their distributions (Figure 9), although some extremes might only be replicated within a relatively small proportion of the ensemble runs.

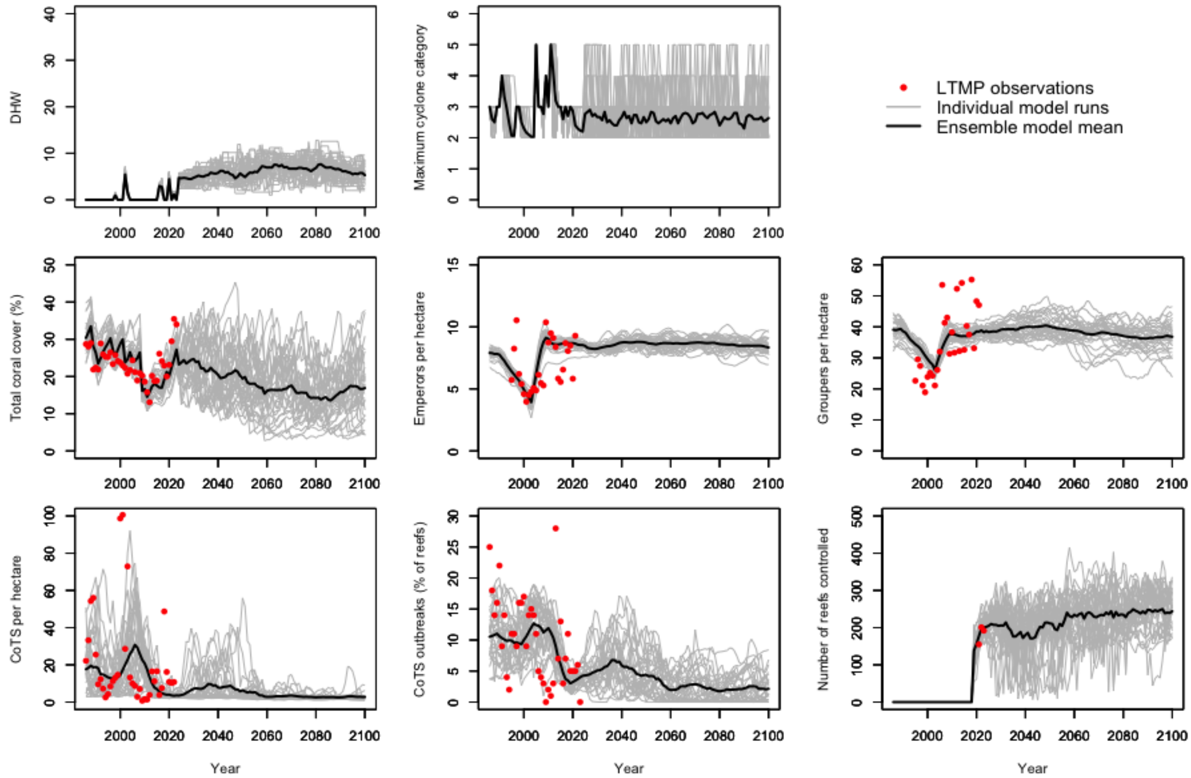

Figure 6: Counterfactual time series (1986-2100) under climate scenario SSP1-2.6. Shown are degree heating weeks (DHW); maximum cyclone category; total coral cover; emperor density; grouper density; CoTS density; CoTS outbreak rate (percentage of reefs > 15 CoTS per ha); and number reefs controlled (with 5 vessels). Each plot shows GBR means from 30 CoCoNet model runs (grey) and the ensemble mean (black). GBR mean LTMP values are also shown for the period 1986-2023 (red).

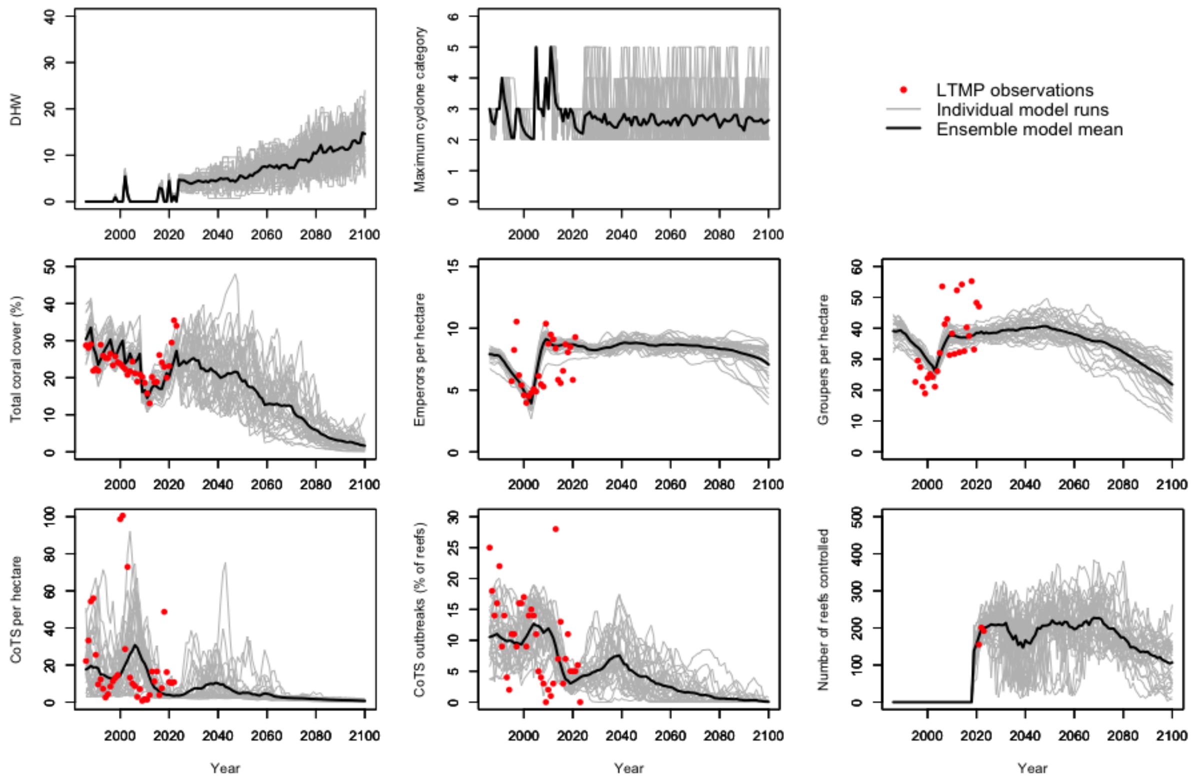

Figure 7: As in Figure 6 for climate scenario SSP2-4.5.

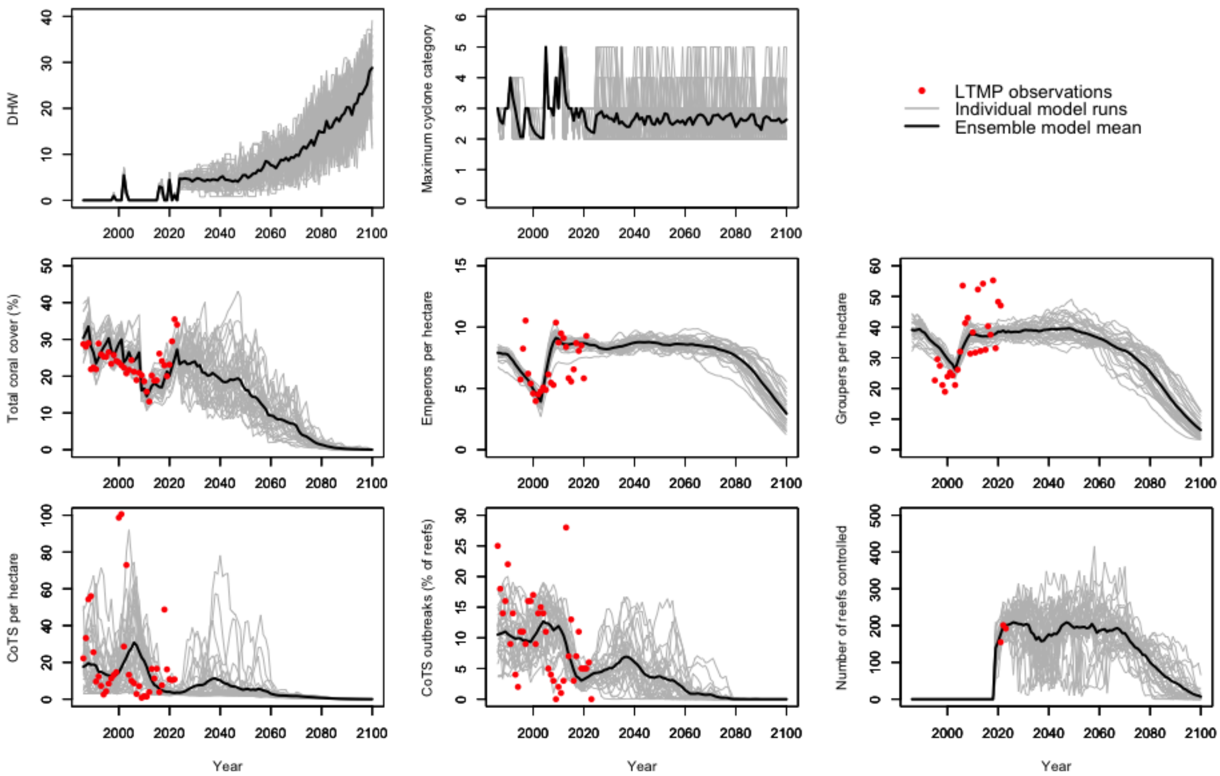

Figure 8: As in Figure 6 for climate scenario SSP3-7.0.

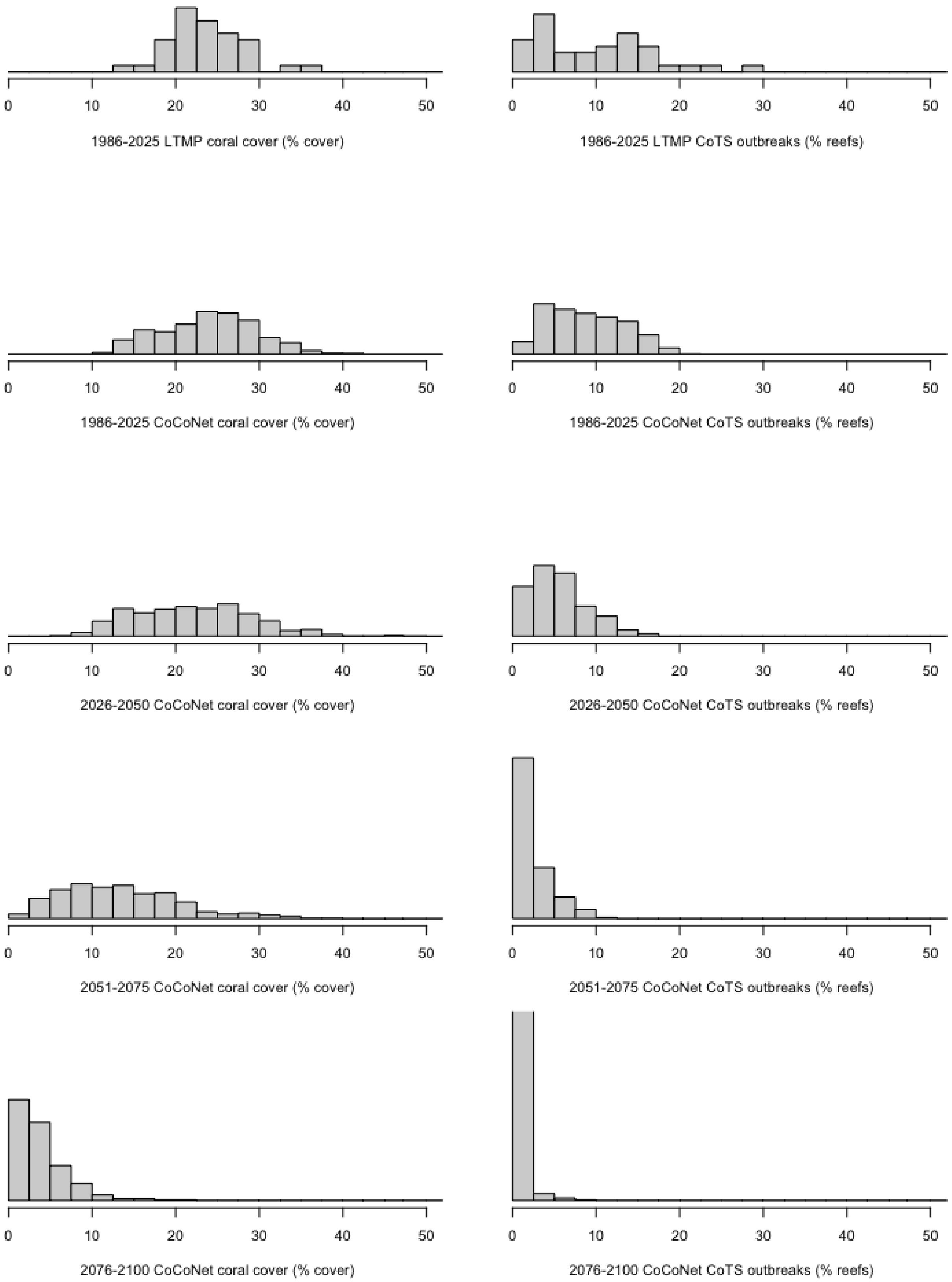

Figure 9: Histograms of GBR means of coral cover (left) and CoTS outbreaks (right). Rows correspond to LTMP data over the periods 1986-2023; CoCoNet results for the period 1986-2025; CoCoNet results for the period 2026-2050; CoCoNet results for the period 2051-2075; and CoCoNet results for the period 2076-2100. The maximum bar height corresponds to 0.3 (as indicated in the bottom right histogram).

2.6 Counterfactual scenarios

The calibrated CoCoNet model has been used to generate ensemble hindcasts (2000-2025) and future projections (2026-2100) under three CMIP6 climate scenarios (SSP1-2.6, SSP2-4.5, SSP3-7.0). These included historical conservation zoning, fisheries management and CoTS control, which were all assumed to continue without modification from 2025. Together, these ensemble runs form a set of counterfactuals that can be used as baselines to evaluate the effect of interventions included in future model runs.

All ensembles used an identical sequence of seeds within the random number generator to initiate each run. This ensured that intervention runs have identical environmental forcing to a paired counterfactual run, allowing any differences to be unambiguously attributed to the intervention.

Results from the counterfactual scenarios can be summarised as follows:

- SSP1-2.6 (Figure 6): coral cover declines until 2060, before beginning to recover late in the century. CoTS follow the trends of their coral prey with fewer less intense outbreaks after 2060. Fish stocks show only a slight decline in response to reduced coral cover.
- SSP2-4.5 (Figures 7 and 9): coral cover declines throughout the remainder of the 21st century, with complete collapse of coral and CoTS populations by 2100. Fish stocks also decline, albeit more gradually.
- SSP3-7.0 (Figure 8): coral cover declines at an increasing rate, with complete collapse of coral and CoTS populations by 2080. Fish stocks are more persistent, but severely depleted by 2100.

2.7 Interventions

A range of intervention scenarios have also been implemented within CoCoNet (Table 8). Most are based on relatively simplistic representations that can be refined in the future as relevant data becomes available. They can each be deployed in any year and multiple interventions can be run simultaneously using the model interface.

For most interventions, reefs are prioritised following a list generated by the CoTS Control Program (Matthews et al. 2024). Priority reefs are those that have economic (e.g. as tourism sites) or ecological value (e.g. as larval source reefs) and are vulnerable to COTS during any of the stages of the outbreak wave. Logistical factors are also considered in the prioritisation process. The model uses the reef priority list generated by the CoTS control program in 2024.

The deployment region for interventions can also be restricted to a geographical box specified in terms of latitudinal and longitudinal ranges.

Catchment restoration has been a major focus of GBR restoration initiatives since 2003 (Brodie et al. 2012, Kroon et al. 2016). The model represents associated improvements in coastal water quality by reducing the offshore scale for turbidity impacts on coral growth rates associated with storm and cyclone events. Catchment restoration is assumed to improve water quality over any specified timeframe measured in years.

Starfish control based on Integrated Pest Management principles has operated on the GBR since 2018 (Babcock et al. 2020, Westcott et al. 2020, Rogers et al. 2023, Matthews et al. 2024), whereby target reefs are intensively controlled until an ecological threshold is reached and then maintained by periodic surveillance. Each year the model replicates this process following the priority list until the annual control capacity, set by the number and diver capacity of control vessels, had been fully utilised (Castro-Sanguino et al. 2023). The effort required to control each reef site to the CoTS density threshold (equation 8a) is dependent on the pre-existing CoTS density (equation 8b). Once a site has been controlled, it continues to be monitored and controlled while ever the control program continues to operate.

Conservation zoning was first applied on the GBR in 1987 when approximately 150 reefs were closed to fishing, with more than 1000 additional reefs declared as no-take protected zones in 2004 (Day 2008). The model assumes full compliance with zoning regulations by setting catches to zero on protected reefs, where levels of illegal fishing have been reported to be low (Davis et al. 2004). As well as representing historical changes in protection, the model can represented expansion in the number of reefs protected starting with the highest priority reefs.

Fisheries catch regulations on the GBR have evolved over the past 30 years through changes in commercial licenses, quotas, gear restrictions, and seasonal closures (Brown et al. 2020). Future catches in the model can be reduced by any specified fraction.

Fisheries size regulations have been applied on the GBR since 1996. Further restrictions on upper or lower size limits of emperors and groupers can be specified in the model. In this context, age is used a proxy for size, with one additional age-class excluded from the fishery in each case.

Fish replenishment involved breeding predatory species of finfish in aquaculture facilities and releasing them back onto the reef. This strategy has never been deployed on the GBR. However, the model allows for release of a specified number of juvenile emperors on a specified number of priority reefs where emperors stocks are depleted.

Coral replenishment involves harvesting of wild coral spawn slicks, culturing of the coral larvae within onboard aquaculture facilities during transit, and final release of mature larvae onto reefs targeted for restoration. This approach has been tested on the GBR at small scale (Doropoulos et al. 2019). In the model, juvenile corals with the thermal tolerance characteristics from a selected spawn collection reef are transferred to other priority reefs.

Coral enhancement involves selective breeding of corals in aquaculture facilities to enhance their levels of thermal tolerance, before outplanting juveniles back onto the reef. These processes are currently being tested on the GBR (Anthony et al. 2017). However, the model allows for outplanting of a specified cover of a thermally tolerant coral group on priority reefs where coral cover is depleted.

Coral rubble stabilisation has previously only been undertaken on the GBR at very small scales (Ceccarelli et al. 2020). In the model, a specified area of rubble is stabilised on a specified number of priority reefs where rubble cover is above a specified threshold.

Local shading involves artificial fog generation at individual reefs to reflect solar radiation. This approach has been deployed experimentally on the GBR (Sovacool et al. 2023). It is represented in the model as a proportional reduction in DHWs on a specified number of reefs.

Regional shading (cloud brightening) involves the generation of artificial sea spray aerosol to enhance coral cover and reflect solar radiation. This approach has been deployed experimentally on the GBR (Hernandez-Jaramillo et al. 2025). It is represented in the model by reducing DHWs over a specified region.

Modification of local pH levels has not previously been deployed on the GBR. It is represented in the model by moderating the fall in coral growth rates and increased susceptibility to storm damage associated with ocean acidification.

Table 8 Description of interventions implemented in CoCoNet. The model allows the start year of each intervention to be specified independently. Where capacity is specified in terms of the number of deployment reefs, reefs are selected randomly from target reefs, then from remaining priority reefs, then from non-priority reefs (as defined by the GBRMPA).

Intervention	Effect of intervention	Capacity specification
Catchment restoration	Reduce flood effects on growth of inshore corals.	Catchment restoration timeframe.
Starfish control	Reduce CoTS densities on controlled reefs.	Annual number of control vessels in each zone and/or outbreak front, and thresholds for maximum coral and minimum CoTS.
Conservation zoning	Change status of reefs from Blue (fishing permitted) to Green (fishing excluded).	Number of reefs with changed status.
Fisheries catch regulations	Reduce total catch by commercial and recreational fishing on the GBR.	Fractional reduction in total catch.
Fisheries size regulations	Ban fishing of youngest and/or oldest age-class of both fish groups.	Applied to all reefs.
Fish replenishment	Supplement populations of juvenile emperors.	Annual number of reefs, number released on each reef, and threshold for maximum existing adults.
Coral replenishment	Translocate coral larvae from one reef to another.	Annual number of reefs, total area settled, and threshold for maximum existing coral cover.
Coral enhancement	Outplant corals with higher thermal tolerance than natural population.	Annual number of reefs, total area outplanted, and threshold for maximum existing coral cover.
Coral rubble stabilisation	Reduce rubble cover.	Annual number of reefs, total area stabilised, and threshold for minimum rubble cover.
Local shading (fogging)	Reduce DHW exposure on individual reefs.	Annual number of reefs, reduction in DHW exposure.
Regional shading (cloud brightening)	Reduce DHW exposure over intervention region.	Reduction in DHW exposure.
Modification of local pH levels	Reduce effect of ocean acidification on coral growth.	Annual number of reefs and proportional reduction in effect of ocean acidification on coral growth rate.

Appendix A System requirements

The functional requirements of the CoCoNet modelling system are as follows.

(i) The modelling system must be version controlled and available for download online.
(ii) Saved outputs must resolve annual conditions at the scale of individual reefs, which corresponds to the fundamental management unit for the GBR.
(iii) Saved outputs must be readable by common analysis tools such as Microsoft Excel and R.
(iv) Documentation must include a User Guide and transparent descriptions of the underlying theory and model assumptions.

Non-functional requirements of the CoCoNet modelling system are as follows.

(i) The modelling system should be portable, running on common computing platforms such as PC, Mac and HPC systems.
(ii) The model should complete typical ensemble runs (~ 30 runs x 100 years) within 24 hours on an average desktop computer.
(iii) Model code should be computationally efficient, readable, and fully documented.

Appendix B Model equations

Table A.1 Model equations relating to age-stuctured CoTS populations and coral functional groups (sa = staghorn acropora; ta = tabular acropora; tt = thermally tolerant; mo = montipora; po = poritidae; fa = favids.

Description	Equation	Assumptions	
Crown-of-thorns starfish population dynamics			
CoTS: age 0	$S_{y+1,0} = \alpha^S R_y e^{-\left(S_{allee}/(S_{y,2}+S_{y,3}+S_{y,4}+S_{y,5}+S_{y,6+})\right)^{0.5}} \left(\lambda(S_{y,2} + 2S_{y,3} + 4S_{y,4} + 8S_{y,5} + 8S_{y,6+}) + (1-\lambda)\sum_{reefs} \mathrm{K}_y^S(\dot{S}_{y,2} + 4\,\dot{S}_{y,3} + 16\,\dot{S}_{y,4} + 32\dot{S}_{y,5} + 32\dot{S}_{y,6+})\right)$	Fecundity of CoTS doubles with each size class (Pratchett et al. 2021) before plateauing at 6-years with senescent phase. Allee effects apply at low CoTS densities (Rogers et al. 2017) CoTS settlement limited to rubble area in part due to predation and stinging by corals (Wilmes et al. 2020).	1a
CoTS: age 1	$S_{y+1,1} = \left(S_{y,0} + S_{y,1}\left(1 - {C_y^f}^{0.5}\right)\right) e^{-\left(M_1^S/R_y\right)} - q_{y,1}^{SB} - q_{y,1}^{SE}$	Natural mortality of juvenile CoTS dependent on availability of their preferred coral rubble habitat.	1b
CoTS: age 2	$S_{y+1,2} = S_{y,1} {C_y^f}^{0.5} e^{-\left(M_2^S/C_y^f\right)} - q_{y,2}^{SE} - H_{y,2}^S$	Fraction of juvenile CoTS that transition to adults is dependent on availability of preferred coral (Deaker et al. 2020).	
CoTS: age a = 3:5	$S_{y+1,a} = S_{y,a-1} e^{-\left(M_a^S/C_y^f\right)/(a-1)} - q_{y,a}^{SE} - H_{y,a}^S$	Adult CoTS mortality decreases with both age (Keesing et al. 2018, Rogers and Plaganyi 2022) and availability of fast-growing coral as their preferred prey (Pratchett 2010).	1c
CoTS: age 6+	$S_{y+1,6+} = (S_{y,5} + S_{y,6+}) e^{-\left(M_{6+}^S/C_y^f\right)} - q_{y,a}^{SE} - H_{y,6}^S$	CoTS mortality increases again at 6-years with senescent phase (Pratchett et al. 2014), while continuing to depend on coral availability.	1d
Terms for predation on CoTS			
Predation of juvenile CoTS by benthic invertebrates	$q_{y,1}^{SB} = \dfrac{p_1^{SB} S_{y,1} B_y}{S_{y,1} + p_1^{SB} B_y}$	Predation can be limited by juvenile CoTS abundance or handling time (Wilmes et al. 2018).	2a
Predation of CoTS by emperors	$q_{y,a}^{SE} = \frac{p_a^{SE} S_{y,a} E_y e^{-(\delta_{a,1} R_y)}}{S_{y,a} + p_a^{SE} E_y}$, $E_y = \frac{1}{15}(E_{y,1} + 2E_{y,2} + 3E_{y,3} + 4E_{y,4} + 5E_{y,5})$, $\delta_{a,1} = \begin{cases} 1; a = 1 \\ 0; a \neq 1 \end{cases}$	Predation increases with emperor age and can be limited by CoTS abundance or handling time (Dunic and Baum 2017). Rubble provides juvenile CoTS with a refuge from emperor predation (Keesing 1995, Wilmes et al. 2018).	2b
Coral population dynamics			
Coral groups	$C_{y+1}^g = C_y^g\left(1 + r_y^g - M_y^{g,Cyc} - M_y^{g,Ble} - q_y^{gS}\right) + \sum_{reefs} \alpha^C \mathrm{K}_y^C C_y^g \left(r_0^g/r_y^g\right) e^{-\left(C_{allee}/C_y^g\right)^{0.5}}$ $(g = sa, ta, tt, mo, fa, po)$	Recruitment of coral is limited by competition (Evensen et al. 2021) and declines with OA following growth rate (Smith et al. 2020). Allee effects apply at low cover of any coral group (Mumby et al. 2024).	3a

Description	Equation	Assumptions	
Structural coral cover	$C_y^f = C_y^{sa} + C_y^{ta} + C_y^{tt} + C_y^{mo}$		3b
Total coral cover	$C_y = C_y^{sa} + C_y^{ta} + C_y^{tt} + C_y^{mo} + C_y^{fa} + C_y^{po}$	Definition	3c
Coral diversity (evenness index)	$\mathcal{J} = -\frac{1}{ln(5)}\left(C_y^{sa} ln\left(C_y^{sa}\right) + C_y^{ta} ln\left(C_y^{ta}\right) + C_y^{mo}\, ln\left(C_y^{mo}\right) + C_y^{po} ln\left(C_y^{po}\right) + C_y^{fa} ln\left(C_y^{fa}\right)\right)$	Definition (excludes introduced thermally tolerant corals).	3d
Rubble cover	$R_{y+1} = R_y\left(1 - r^{consol}\right) + \sum_g C_y^g\left(M_y^{g,Cyc} + M_y^{g,Ble}\right)$	Rubble accumulation is driven by cyclone and bleaching events and is limited by consolidation.	3e
Terms for predation on coral			
Coral groups	$q_y^{gS} = p^{CS} S_y$ if $p^{CS} S_y < S_{pref} C_y^g$, $S_y = 0.2S_{y,1} + S_{y,2} + 2S_{y,3} + 4S_{y,4} + 8S_{y,5} + 8S_{y,6+}$ With predation applied sequentially for $(g = sa, ta, tt, mo, fa, po)$	Consumption of coral increases with the age class of CoTS (Keesing and Lucas 1992). CoTS consume faster-growing corals first (Pratchett 2010).	4a
Fish population dynamics			
Benthic invertebrates	$B_{y+1} = B_y\left(1 + r_0^B\left(1 - B_y/K_B\right) - q_y^{BT}\right)$	Recruitment is limited by carrying capacity. Limited evidence from other regions (Rodriguez-Troncoso et al. 2019).	5a
Triggerfish (and cardinalfish)	$T_{y+1} = T_y\left(1 + r_0^T\left(1 - T_y/K_T\right) - q_y^{TG}\right)$	Recruitment is limited by territorial behaviour (Bean et al. 2002).	5b
Emperors age *a* = 0	$E_{y+1,0} = \alpha_y^E\left(\left(E_{y,4} + 2E_{y,5}\right) + \sum_{reefs}\left(\dot{E}_{y,4} + 2\dot{E}_{y,5}\right)\right)$	Emperors breed from age 4-years with larval production doubling for each age-class. Juveniles come from local reefs via seagrass nursery grounds (no larval retention).	5c
Emperors age *a* = 1	$E_{y+1,1} = E_{y,0}$	Recruitment is modelled only for fish surviving at least to age 1.	5d
Emperors age *a* = 2:5	$E_{y+1,a} = E_{y,a-1}\left(1 - \frac{M^E}{(a-1)\left(1 + C_y\right)} E_{y,a-1}\right) - F_{y,a}^E$	Quadratic mortality term. Mortality rate decreases with age and coral cover.	5e
Groupers age *a* = 0	$G_{y+1,0} = \alpha^G\left(\lambda\left(G_{y,2} + 2S_{y,3} + 4G_{y,4} + 8S_{y,5}\right) + (1 - \lambda)\sum_{reefs} \mathrm{K}_y^G\left(\dot{G}_{y,2} + 2\dot{G}_{y,3} + 4\dot{G}_{y,4} + 8\dot{G}_{y,5}\right)\right)$	Groupers breed from age 2-years with larval production doubling for each age-class.	5f
Groupers age *a* = 1	$G_{y+1,1} = G_{y,0}$	Recruitment is modelled only for fish surviving at least to age 1.	5g
Groupers age *a* = 2:5	$G_{y+1,a} = G_{y,a-1}\left(1 - \frac{M^G}{(a-1)} G_{y,a-1}\right) - F_{y,a}^G$	Quadratic mortality term. Mortality rate decreases with age and coral cover.	5h
Terms for predation on fish			
Predation of benthic invertebrates by triggerfish	$q_y^{BT} = \frac{p^{BT} T_y}{B_y + p^{BT} T_y} e^{-\left(C_y + R_y\right)}$	Predation is reduced by coral and rubble cover (Fabricius et al. 2014). Predation can be limited by benthic invertebrate abundance or handling time.	6a
Predation of triggerfish by groupers	$q_y^{TG} = \frac{p^{TG} G_y}{T_y + p^{TG} G_y} e^{-C_y}$, $G_y = \frac{1}{15}\left(G_{y,1} + 2G_{y,2} + 3G_{y,3} + 4G_{y,4} + 5G_{y,5}\right)$	Predation increases with grouper age and is reduced by coral cover.	6b

Table A.2 Model equations for environmental effects on corals.

Description	Equation	Assumptions	No.
Terms for environmental effects on coral	$(\boldsymbol{g = sa, ta, tt, mo, fa, po})$		
Fraction of larvae retained on reefs	$\lambda = e^{-50/sites^{0.5}}$	Estimate based on high-resolution particle tracking experiments (Jim Greenwood, personal communication).	7a
Maximum cyclone induced mortality	$M_y^{g,Cyc} = \min\left(1.0, \left(0.28CAT_y - 0.24\right) r_0^g / r_y^g\right) \quad (g = sa, ta, tt)$ $M_y^{mo,Cyc} = 0.5\left(M_y^{sa,Cyc} + M_y^{fa,Cyc}\right) \quad (g = mo)$ $M_y^{g,Cyc} = \left(0.074CAT_y^2 - 0.24CAT_y + 0.24\right) r_0^g / r_y^g \quad (g = fa, po)$	Cyclone mortality is higher for fast-growing corals than slow-growing corals (Condie et al. 2018). Cyclone mortality increases as growth rates fall with ocean acidification (Madin et al. 2012), approximately doubling by 2100 under SSP2-4.5.	7b
Maximum bleaching induced mortality	$M_y^{g,Ble} = 1 - e^{\left(-0.1e^{0.3max\left(0, DHW_y - \mathcal{S}_y - \mathcal{T}_y^g\right)}\right)}$	Bleaching mortality is dependent on DHW exposure and the thermal tolerance of corals. Data from Sam Matthews suggest significantly lower mortality than shallow coral estimates (Hughes et al. 2017). Mortality at each reef is varied randomly [0.5 1.0]$M_y^{g,Ble}$.	7c
Intrinsic thermal tolerance	$\mathcal{T}_0^g = 3.5 - 5r_0^g$	Slower growing corals have higher thermal tolerance than faster growing corals (Muir et al. 2017).	7d
Thermal tolerance adaptation after bleaching	$\mathcal{T}_{y+1}^g = min\left(\mathcal{T}_y^g (1 + \mathcal{A})^{M_y^{g,Ble}}, \mathcal{T}_0^g + \mathcal{P}\right)$	The average thermal tolerance of corals surviving a bleaching increases within an upper bound (Matz et al. 2018).	7e
Influence of thermal adaptation and ocean acidification on growth	$r_{y+1}^g = \left(r_y^g \left(1 - 0.01\left(\mathcal{T}_y^g - \mathcal{T}_0^g\right)\right)\right)^{OA}$	Increased thermal tolerance is associated with lower coral growth rates. Growth rates fall with increasing ocean acidification.	7f
Ocean acidification influence on cyclone damage and coral growth	$OA = 1 + k^g(1 - P^{OA})RCP^{0.5}$	Ocean acidification effects are larger on faster-growing corals (Comeau et al. 2014) and increase with climate change.	7g

Table A.3 Model equations for control of CoTS and fishing.

Description	Equation	Assumptions	No.
CoTS control			
Ecological threshold (for coral decline)	$S_{y,ecol} = 7.2$	Empirical estimate based on number of reefs controlled historically.	8a
Control dives (to reach ecological threshold)	$\mathcal{D}i_y = 4.18\left(\frac{S_{y,2}+S_{y,3}+S_{y,4}+S_{y,5}+S_{y,6+}}{\alpha}\right)^{0.67}$	Empirical relationship (analysis by Dan Gladish, CSIRO, personal communication).	8b
Fisheries catches			
Annual catch of emperors	$Catch_y^E = \frac{600000}{Rep_{<2004}^E}\, max\left(1.0\,,\ 2.5\left(1-e^{-0.01e^{0.08(y-1940)}}\right)\right) \quad (y < 2004)$ $Catch_y^E = \frac{400000}{Rep_{\geq 2004}^E} \quad (y \geq 2004)$	Empirical fit to aggregated confidential reef-scale fisheries data.	8c
Annual catch of groupers	$Catch_y^G = \frac{1160000}{Rep_{<2004}^G}\, max\left(1.0\,,\ 2.5\left(1-e^{-0.01e^{0.08(y-1940)}}\right)\right) \quad (y < 2004)$ $Catch_y^G = \frac{900000}{Rep_{\geq 2004}^G} \quad (y \geq 2004)$	Empirical fit to aggregated confidential reef-scale fisheries data.	8d

Table A.4 Definition of model variables.

Variable	Definition
Crown-of-thorns starfish	(age: a = 0, 1, 2, 3, 4, 5, 6+)
$\boldsymbol{S_{y,a}}$	Number of CoTS of age *a* at the start of year *y* ($\dot{S}_{y,a}$ for connected reefs)
$\boldsymbol{H^{S}_{y,a}}$	Fraction of CoTS of age *a* removed through control programs during year *y*
$\mathbf{K}^{S}_{y}$	Dispersal kernel elements for CoTS
Coral groups	(group: $g = sa, ta, mo, tt, fa, po$)
$\boldsymbol{C^{g}_{y}}$	Cover of coral group g at the start of year *y* ($\dot{C}^{g}_{y}$ for connected reefs)
$\boldsymbol{C_{y}}$	Total coral cover at the start of year *y*
$\boldsymbol{R_{y}}$	Coral rubble cover at the start of year *y*
$\boldsymbol{M^{g,Cyc}_{y}}$	Cyclone induced mortality of coral group g in year *y*
$\boldsymbol{M^{g,Ble}_{y}}$	Bleaching induced mortality of coral group g in year *y*
$\boldsymbol{\mathcal{T}^{g}_{y}}$	Thermal tolerance (in DHW) of coral group g in year *y*
$\mathbf{K}^{C}_{y}$	Dispersal kernel elements for corals
Fish groups	(age: a = 0, 1, 2, 3, 4, 5+)
$\boldsymbol{E_{y,a}}$	Number of emperors of age *a* at the start of year *y* ($\dot{E}_{y,a}$ for connected reefs)
$\boldsymbol{G_{y,a}}$	Number of groupers of age *a* at the start of year *y* ($\dot{G}_{y,a}$ for connected reefs)
$\boldsymbol{Catch^{E}_{y}}$	Catch of emperors in year *y* distributed across ages $a \geq 3$ (kg)
$\boldsymbol{Catch^{G}_{y}}$	Catch of groupers in year *y* distributed across ages $a \geq 3$ (kg)
$\mathbf{K}^{G}_{y}$	Dispersal kernel elements for groupers
Environmental conditions	
$\boldsymbol{CAT_{y}}$	Cyclone category within year *y* (1, 2, 3, 4, 5)
$\boldsymbol{DHW_{y}}$	Degree heating weeks at a reef over year *y*
Other interventions	
$\boldsymbol{S_{y}}$	Effect of artificial shading or cooling (in DHW) at a reef over year *y*
$\boldsymbol{P^{OA}}$	Level of artificial protection from ocean acidification [0 1]

Table A.5 Model parameter values.

Parameter	Description	Value	Estimation method	Reference
Crown-of-thorns starfish				
α^S	Maximum recruitment per CoTS (a = 2) on natal reefs	300000	Fitted to LTMP	(Caballes et al. 2017)
S_{allee}	CoTS density e-folding scale for Allee effects	3	Empirical data	(Rogers et al. 2017)
M_a^S	Natural mortality of CoTS age a when preferred coral is abundant	0.8 (a =1,6) 0.0 (a =2-5)	Fitted to LTMP	-
p_1^{SB}	Juvenile CoTS consumed per benthic invertebrate per year	500	Pre-specified	Plausible estimate
p_1^{SE}	Juvenile CoTS consumed per emperor per year	500	Pre-specified	Plausible estimate
p_a^{SE}	Adult CoTS consumed per emperor per year ($a \geq 2$)	50	Pre-specified	Plausible estimate
ϵ	Conversion factor: control program CoTS ha^{-1} to CoTS per manta tow	0.015	Pre-specified	(Moran and Death 1992)
Coral groups				
r_0^{sa}	Intrinsic growth rate (including local recruitment) in year *y*	0.50 yr^{-1}	Pre-specified	(Hughes et al. 2018)
r_0^{ta}	Intrinsic growth rate (including local recruitment) in year *y*	0.40 yr^{-1}	Pre-specified	(Hughes et al. 2018)
r_0^{tt}	Intrinsic growth rate (including local recruitment) in year *y*	0.40 yr^{-1}	Pre-specified	(Hughes et al. 2018)
r_0^{mo}	Intrinsic growth rate (including local recruitment) in year *y*	0.30 yr^{-1}	Pre-specified	(Hughes et al. 2018)
r_0^{po}	Intrinsic growth rate (including local recruitment) in year *y*	0.15 yr^{-1}	Pre-specified	(Hughes et al. 2018)
r_0^{fa}	Intrinsic growth rate (including local recruitment) in year *y*	0.10 yr^{-1}	Pre-specified	(Hughes et al. 2018)
α^C	Maximum recruitment of coral group g from connected reefs	0.05	Fitted to LTMP	-
C_{allee}	Coral density e-folding scale for Allee effects	0.02	Empirical data	(Mumby et al. 2024)
K_C	Coral carrying capacity	1.0	By definition	-
p^{CS}	Consumption rate of coral by COTS	0.0003	Empirical data	-
r^{consol}	Consolidation rate of coral rubble	0.17 yr^{-1}	Pre-specified	(Biggs 2013)
Fish groups				
K_B	Carrying capacity of benthic invertebrate CoTS predators	10000 ha^{-1}	Pre-specified	Plausible estimate
K_T	Carrying capacity of triggerfish	200 ha^{-1}	Pre-specified	(Kavanagh and Olney 2006)
α^B	Benthic invertebrate recruitment	0.5	Pre-specified	Plausible estimate
α^T	Triggerfish recruitment	0.8	Pre-specified	Plausible estimate
α^E	Emperor recruitment	0.0028	Fitted to LTMP	-
α^G	Grouper recruitment	4.0	Fitted to LTMP	-
M^G	Natural mortality of groupers	0.01	Pre-specified	(Little et al. 2008, Mapstone et al. 2008)
M^E	Natural mortality of emperors	0.026	Pre-specified	(Little et al. 2008)
p^{BT}	Maximum benthic invertebrates consumed per triggerfish per year	120	Pre-specified	Plausible estimate
p^{TG}	Maximum triggerfish consumed per grouper per year	70	Pre-specified	Plausible estimate

Parameter	Description	Value	Estimation method	Reference
Environmental effects on corals				
$\boldsymbol{RCP}$		Climate scenario	2.6 (SSP1-2.6) 4.5 (SSP2-4.5) 7.0 (SSP3-7.0)	Pre-specified (McWhorter et al. 2022)
$\boldsymbol{\mathcal{A}}$	Adaptability of corals to thermal stress (if $\boldsymbol{\mathcal{A}}$ = 1, thermal tolerance of corals doubles as mortality approaches 100%)	1	High if shuffling symbionts	Pre-specified
$\boldsymbol{\mathcal{P}}$	Maximum thermal plasticity of corals (high uncertainty, some consensus that >10 DHW is highly unlikely on relevant timescales)	8 DHW	Loose consensus of geneticists	Pre-specified
$\boldsymbol{k^{sa}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0025	Pre-specified	(Albright et al. 2010, Dove et al. 2013)
$\boldsymbol{k^{ta}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0020	Pre-specified	(Albright et al. 2010, Dove et al. 2013)
$\boldsymbol{k^{mo}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0005	Pre-specified	(Browne 2012, Dove et al. 2013)
$\boldsymbol{k^{po}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0010	Pre-specified	(Dove et al. 2013, Fabricius et al. 2017)
$\boldsymbol{k^{fa}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0020	Pre-specified	(Dove et al. 2013)
$\boldsymbol{k^{tt}}$	Factor controlling decline in coral growth and recruitment from ocean acidification	0.0010	Pre-specified	(Dove et al. 2013)

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CONTACT US

t 1300 363 400
+61 3 9545 2176
e enquiries@csiro.au
w www.csiro.au

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CSIRO Environment
Scott Condie
t +61 3 6232 5025
e scott.condie@csiro.au
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