COTS Control Innovation Program

TECHNICAL REPORT

Fish predator conservation to prevent crown-of-thorns starfish (COTS) outbreaks

Daniela Ceccarelli, Leanne Currey-Randall, Scott Condie, Diego Barneche, Javier Porobic, Michael Emslie

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COTS Control Innovation Program | A research and development partnership to better predict, detect and respond to crown-of-thorns starfish outbreaks

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Traditional Owner Acknowledgement

The COTS Control Innovation Program extends its deepest respect and recognition to all Traditional Owners of the Great Barrier Reef and its Catchments, as First Nations Peoples holding the hopes, dreams, traditions and cultures of the Reef.

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Acronyms and Abbreviations

AIMS	Australian Institute of Marine Science
CC	COTS Control (Program)
CCIP	Crown-of-thorns starfish Control Innovation Program
CoCoNet	Coral Community Network model
COTS	Crown-of-thorns starfish
DNA	Deoxyribonucleic acid
GBR	Great Barrier Reef
GBRF	Great Barrier Reef Foundation
GBRMP	Great Barrier Reef Marine Park
HDI	Highest Density continuous Interval
IMR	Integrated Monitoring and Reporting
IPM	Integrated Pest Management
IQR	Inter Quartile Range
JCU	James Cook University
LTMP	Long-Term Monitoring Program
MICE	Model of Intermediate Complexity for Ecosystem assessments
MPA	Marine Protected Area
QLD DPI	Queensland Department of Primary Industries (previously Queensland Department of Agriculture and Fisheries)
RRAP	Reef Restoration and Adaptation Program
SSP	Shared Socioeconomic Pathways
The Reef Authority	Great Barrier Reef Marine Park Authority
TO	Traditional Owner

EXECUTIVE SUMMARY

In an era of increasing human pressure on coral reefs, crown-of-thorns starfish (*Acanthaster* spp., or COTS) outbreaks have been a leading cause of coral mortality throughout the Indo-Pacific. The Great Barrier Reef (GBR) is subject to repeated COTS outbreaks causing widespread damage. While solutions to more difficult issues such as climate change-driven mass coral bleaching will take longer to be actualised, COTS control is one method to protect corals—the GBR's ecosystem engineers—while we bridge the gap between the concerning trajectories in reef degradation of the present, and a future where climate change is brought under control. As a result, an extensive and successful COTS Control Program has been developed.

This COTS Control Innovation Program (CCIP) project aimed to quantitatively assess whether protecting fish that prey on COTS or impact COTS through trophic pathways could effectively reduce COTS outbreaks and protect coral cover on the GBR. Using a sophisticated modelling approach (the Coral Community Network model, or CoCoNet), we evaluated both the historical effectiveness of existing management measures and the potential benefits of various future management scenarios focused on enhancing the populations of fish that affect COTS through the food chain (primarily emperors and groupers). Using CoCoNet to evaluate biocontrol scenarios for COTS control involved two steps. Firstly, the CoCoNet model capability was enhanced with additional parameters by including benthic invertebrates that prey on juvenile COTS, key groups of fish that affect COTS numbers through the food chain, fisheries data, and environmental forcing in the form of ocean currents, tropical cyclones, flood plumes and marine heatwaves. CoCoNet was also updated with the latest connectivity information, and with empirical evidence emerging from other CCIP projects, such as predation rates on different life stages of COTS. Secondly, the updated model was then used to test scenarios simulating various biocontrol interventions designed to affect fish predators (direct and indirect) of COTS (management scenarios).

In addition to a historical scenario and a counterfactual scenario of no management interventions, we tested twelve different future management scenarios, including expanding no-take zones, reducing fishing pressure, and increasing direct COTS control efforts. Top ranking scenarios were prioritised for testing within CoCoNet. Each model run started in 1956 to allow the system to equilibrate. Over the period 1956–2025, historical changes in management were included, culminating in the major rezoning and restructure of fisheries in 2004. Additional management scenarios were then tested in the model from 2026 to 2050. To test the efficacy of historical management, an additional run excluded all past and future management interventions. Every scenario was rerun 20 times, with the timing and magnitude of future events, such as cyclones, heatwaves and COTS spawning, varying stochastically between runs. This 20-member ensemble of runs thereby captured the range of uncertainty associated with future projections. The results were presented as changes in fish densities, coral cover, and the proportion of reefs with COTS outbreaks (> 15 adult COTS per hectare).

The hindcast modelling detected significant gains in emperor and grouper densities and corresponding declines in the proportion of reefs with COTS outbreaks and increases in coral cover as a result of the major zoning and fisheries management practices implemented in 2004. Modelling estimated that the change in Marine Park Zoning from ~4% to ~30% no-take zones and additional fisheries restrictions enacted in 2004 led to substantial gains in the densities of emperors and groupers, a 70% relative median reduction in active COTS outbreaks and a 13% relative median increase in coral cover compared with the counterfactual scenario of no zoning or fisheries management changes. Despite some geographic variations throughout the GBR Marine Park (GBRMP), these changes were detectable at a whole-of-GBR scale. Our forecast modelling results also indicated that deployment of 10 COTS control vessels will likely result in greater reductions in COTS outbreaks than expansion of predator (direct and indirect) conservation measures alone.

Modelling scenarios to forecast the effects of increasing these biocontrol measures offers a low-risk method of assessing the potential benefits of management changes that would be economically, socially and culturally challenging to implement in the real world. Results of these forecasted scenario runs show that direct COTS control using 10 vessels would provide the most immediate and consistent reduction in COTS outbreaks (~36% reduction by 2050) and increasing no-take zones to 40% would provide the greatest coral cover benefits (~8% increase by 2050). However, the benefits to coral were not substantial relative to underlying uncertainties (and variation) in the model projections. Despite the clear benefits to date of existing strategies, forecasts suggest that climate change will overwhelm much of the benefit expected from these biocontrol methods over the next 25 years, even under a relatively optimistic climate scenario.

Coral cover alone does not necessarily equate to reef health, diversity, functioning or resilience, and the results of our models in terms of coral cover gains should be viewed as a starting point from which to investigate multiple additional lines of evidence. Assessing potential options for enhanced biocontrol of coral-eating starfish through the conservation of fish that impact them through the food chain is a critical step in achieving meaningful impact. Our hindcast models suggest that previous interventions, specifically the 2004 GBRMP rezoning plan and fisheries management actions, have made an effective contribution to the efforts of controlling outbreaks and protecting coral cover to date, but the modelled expansions of these actions seem unlikely to provide substantial additional benefits under climate change. This highlights the need for greater pressure to mitigate the effects of climate change for the sustainability of coral reef ecosystems.

1. INTRODUCTION

Crown-of-thorns starfish (*Acanthaster* spp. or COTS) are voracious coral predators, and population outbreaks of COTS can result in localised densities of more than 1,000 ha^{-1}, devastating coral reef ecosystems (Chesher 1969; Pratchett et al. 2017). COTS outbreaks are identified as a major cause of coral loss in the Indo-Pacific (Pearson 1981), and are a leading cause of region-wide coral mortality (De'ath et al. 2012) on the Great Barrier Reef (GBR; by *Acanthaster* cf. *solaris*). Multiple outbreaks have occurred over the past four decades, resulting in extensive decline in coral cover, with each outbreak beginning in the northern sectors of the GBR and propagating southward over the course of 10–15 years. The drivers of these outbreaks are still under debate (Pratchett et al. 2017; Caballes et al. 2024), but the damage is compounded by the very clear destructive effects of escalating climate change. However, COTS are perhaps the only agent of devastating coral loss that lends itself to direct local management actions across large spatial scales, with potential for immediate and tangible effects (Pratchett et al. 2019).

On the GBR, COTS management interventions have primarily focused on manual culling of starfish at individual reef sites. COTS control by the Great Barrier Reef Marine Park Authority (the Reef Authority) has evolved from manual removal of starfish at individual reef sites in the 1980s, to intensive culling at high-value tourism sites, to a multi-million-dollar COTS Control Program with 5–6 vessels deployed to 250 prioritised reefs across the GBR each year (Matthews et al. 2024). The COTS Control Program has undergone continuous and adaptive change, shifting from an economic focus to an environmental value focus with the goal of protecting coral cover (Hewitt and Campbell 2020). The deployment of recent COTS control efforts (Matthews et al. 2024) has benefited from long-term reef monitoring program data (Emslie et al. 2020) and the development of COTS and coral meta-community models (Condie et al. 2021; Castro-Sanguino et al. 2023), which have been instrumental in informing the tracking and prediction of COTS outbreak dynamics.

In addition to direct culling of COTS, other innovative options are being explored to control COTS densities (Høj et al. 2020). One of the more promising options is based on the 'predator-removal hypothesis', which postulates that an important cause of COTS population outbreaks is decreased abundance of COTS predators that at natural population densities would effectively regulate COTS abundance (Endean 1969). Hence, increased conservation and augmentation of these natural predators might provide an effective biocontrol mechanism for COTS (Høj et al. 2020).

Our current understanding of the complex food web, the predators of COTS, and the ability of these predators to control COTS densities, is ever evolving. Giant triton (*Charonia tritonis*) was long considered to be one of the primary predators of COTS (Cowan et al. 2017), however recent data on their consumption rate and preference for other sea star species suggests that they are unlikely to contribute significantly to the control of outbreaks at their current population densities (Motti et al. 2022). Currently, ninety-six species of fish and invertebrates are known to prey on different life stages of COTS (Cowan et al. 2017; Kroon et al. 2020; Wolfe et al. 2023) . Of these, seventy-one coral reef fishes are reported to consume pelagic larvae, benthic juvenile, sub-adult and adult COTS (and injured / moribund / dead individuals), identified from laboratory observations, field-based observations, and recent DNA discoveries (Cowan et al. 2017; Kroon et al. 2020). Recent DNA analysis on fish faecal and gut contents samples identified at least nine fish species (from eighteen reef fishes) not previously known to feed on COTS (Kroon et al. 2020). Whilst only a few fish species are able to kill and consume adult COTS, planktivores can consume their larval stages, and several invertivorous fishes may also prey on juvenile COTS (Cowan et al. 2017; Kroon et al. 2020). Empirical studies on predation rates (of fishes and invertebrates) and frequency will provide further insight into effects of predators on COTS, while current data can be incorporated into modelling.

Fish species that either prey directly on COTS, or influence them indirectly through the food web, include several emperors (*Lethrinus* spp.), and groupers (Serranidae) important to fisheries. For emperors, evidence of direct predation includes COTS remains in gut contents, COTS DNA detected in gut and faecal remains, and field observations of feeding on juvenile, healthy adult, and moribund/dead adult COTS (Cowan et al. 2017; Kroon et al. 2020). In contrast, piscivorous groupers indirectly affect COTS numbers primarily by consuming invertivorous fishes, which in turn benefits their crustacean prey which feed on COTS. These emperors and groupers are targeted by commercial, recreational and indigenous coral reef fisheries on the GBR (Henry and Lyle 2003; Mission et al. 2020; Department of Agriculture and Fisheries 2022) and fisheries catch and biological data exist. GBR Marine Park (GBRMP) zoning and a combination of fisheries management strategies regulates the take of these species, including catch quotas and limits, size limits, seasonal closures, and gear restrictions (Northrop and Campbell 2020), with coral trout (groupers of the genus *Plectropomus*) being the primary commercial target (Fox et al. 2020; Queensland Department of Agriculture and Fisheries 2020). The sustained fisheries for groupers and emperors and the rarity of giant triton due to historical overfishing have been linked to increased COTS outbreaks and supports the central proposition of the 'predator removal hypothesis' (Endean 1969; Sweatman 2008; Babcock et al. 2016; Cowan et al. 2017).

Recent research efforts have focused on understanding drivers and biocontrol methods on COTS outbreaks (Babcock et al. 2016). COTS densities and outbreak frequencies are consistently lower in GBR no-take zones (Sweatman 2008; Kroon et al. 2021), even though no-take zones were not implemented with the goal of COTS management (Fernandes et al. 2005). The hypothesis that no-take protection reduces COTS densities through the trophic web by boosting populations of their predators, including fishery targeted fishes, points to the need to better understand the ecology and predation rates of these natural COTS predators. No-take zones on the GBR primarily benefit predatory fish species targeted by fisheries, such as emperors and coral trout (Emslie et al. 2015). Given that there is an established relationship between the biomass of target fish and COTS densities, this opens the door to a more in-depth investigation of the relationship between these fish species, the fisheries that target them, and how modifying their interaction might influence COTS outbreaks and coral cover.

Exploring methods of biocontrol, specifically investigating how predators can be used to manage COTS outbreaks, is a new and innovative line of research. Kroon et al. (2021) confirmed that the removal of predatory fish (emperors and groupers) from the reef was directly related to increased densities of COTS. This result provides motivation to further investigate whether protecting these fish predators may significantly contribute to the reduction in COTS densities and therefore mitigate coral loss (Kroon et al. 2021). There are several ways to enhance densities of predatory fish, such as fisheries regulations to reduce take (e.g. lowering quotas and possession limits, altering size limits, adding temporary closures), expanding no-take zones, or boosting stocks of key species. These measures are potential avenues to increase fish populations and increase direct and indirect predation effects on COTS, but their relative benefits are difficult to quantify from available empirical data.

Managers require a better understanding of the potential benefits of interventions, particularly those that can be deployed at regional scales. Modelling offers a non-invasive approach to exploring the efficacy of various biocontrol measures and to understand how coral cover responds. This step is critical (Klein et al. 2024) given that large-scale interventions are likely to be costly and controversial, with highly uncertain outcomes (Anthony et al. 2020).

The Coral Community Network (CoCoNet) model was developed to explore the role of physical and ecological drivers of the health of coral reef systems over historical periods and to help understand reef futures under climate change projections and management scenarios (Condie and Porobic 2023). While a range of management interventions have previously been implemented within CoCoNet (Condie et al. 2021), exploring the potential benefits of biocontrol required inclusion of predatory fish and related fisheries in the model by utilising fisheries catch data and reef fish monitoring data. Considering an expanded food web supported exploration of management scenarios related to zoning, fisheries management and stock augmentation, as well as comparisons with the potential benefits of direct COTS control through culling.

The aims of the study were to:

- Identify and test potential management options to support biocontrol of COTS.
- Expand the CoCoNet model to represent the dynamics of predatory fish populations and the fisheries that target those populations by utilising ecological and biological fish data and fisheries data.
- Calibrate the model using a combination of formal parameter estimation and heuristic search against up-to-date fisheries data and empirical observations from the Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP).
- Use the calibrated model to evaluate the management options in terms of enhancing fish stocks, controlling COTS and increasing hard coral cover under a single climate change scenario (SSP1–2.6).

This is the first time these fish management measures are being considered explicitly for their potential value in biocontrol of COTS.

1.1 CCIP: Objectives and impact pathway

The COTS Control Innovation Program (CCIP) aims to boost the capacity to predict, detect and respond to COTS outbreaks at scale across the GBR. The CCIP includes 24 projects addressing key knowledge and capability gaps and ties together COTS biology and ecology, genetics, data science, engineering, modelling, decision science, and social science research (**Figure 1**). The main goal of this project (CCIP-R-10) was to address '*whether large-scale management scenarios including biocontrol can effectively control COTS outbreaks and protect coral cover'* using a well-established system modelling approach to test hypothetical scenarios developed in consultation with stakeholders and end-users.

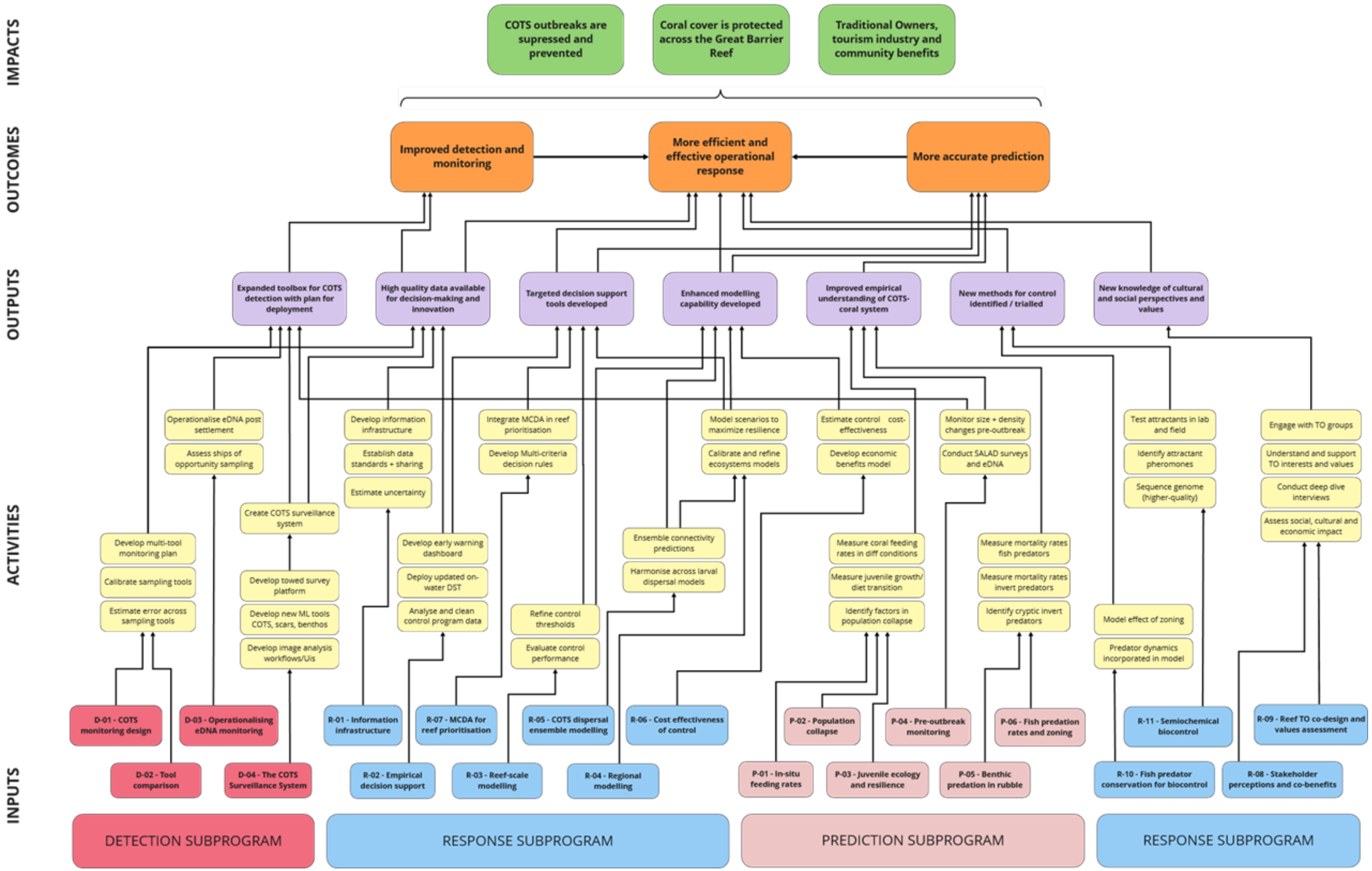

Figure 1. CCIP program logic, showing all the sub-programs included within the program, how the inputs are channelled into activities that produce outputs, which inform outcomes and ultimately add to the three primary intended impacts of the Program. Here we show how the most recent available information on predator dynamics is incorporated into CoCoNet, and then results are considered together with other novel potential control methods (from the testing of semiochemical biocontrol, R-11), discussed with stakeholder (R-08) and TO groups (R-09) and incorporated into improvements in operational response mechanisms. Early results from COTS dispersal modelling (R-05) and empirical predator-prey research (P-01, P-05) were also incorporated where possible.

2. METHODS

2.1 CoCoNet

The CoCoNet model is a meta-community model that includes parameters representing communities of corals and populations of COTS. For this project, additional ecological groups were added, including benthic invertebrates (that prey on juvenile COTS), key fish groups including invertivores (e.g. triggerfish), emperors (e.g. redthroat and spangled emperors) and groupers (e.g. coral trout) (**Figure 2**). Fisheries for emperors and groupers were also incorporated by specifying catches through time based on historical catch data and future catch projections. Ecological processes of growth, mortality and reproduction were included for all groups, with the population age-structures of COTS, emperors and groupers explicitly represented. Populations of all groups are distributed across a network of 3,806 reefs, each resolved at a site-scale encompassing approximately 10 ha of coral habitat, which also equates to the coverage of individual dives undertaken by the COTS Control Program. Many aspects of CoCoNet and its application have been described in detail previously (Condie et al. 2018; Condie et al. 2021; Stoeckl et al. 2021; Condie 2022). The following sections on the use, modification and application of CoCoNet for this project are summarised from Condie and Porobic (2023).

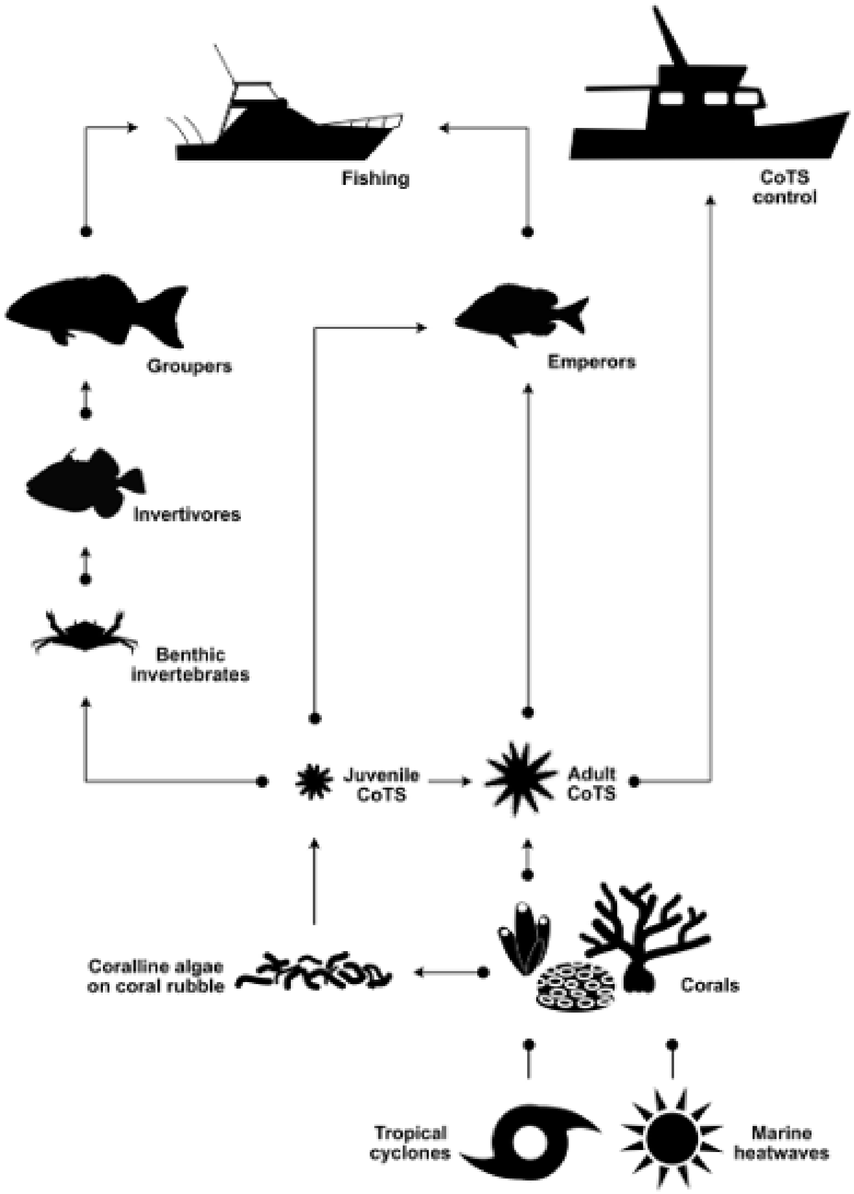

Figure 2. Key components and processes included within the Coral Community Network (CoCoNet) model. Arrows indicate a positive effect and circles a negative effect.

2.1.1 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), marine heatwaves (coral bleaching and mortality), and ocean acidification (reduced coral growth and increased susceptibility to tropical cyclones). Within CoCoNet, the net effect of flood plumes on COTS has been assumed to be small, as any increase in the availability of planktonic food for COTS larvae is likely to be offset by the negative effects of lower-salinity water (Fabricius et al. 2010; Clements et al. 2022). Historical cyclones and heatwaves were applied from 1976 to 2024, followed by stochastic projections from 2025 to 2050. With climate projections revealing no clear trend in future frequency or intensity of cyclones in the GBR region (Knutson et al. 2020), cyclone projections in CoCoNet were based on historical distributions. In contrast, heatwaves in the GBR region increase in all climate projections. Scenarios reported here all used Shared Socioeconomic Pathways SSP1–2.6 (1.8-degree global warming by 2100), which was selected as plausible, but not with such extreme coral bleaching as to mask potential benefits from the modelled predator-related biocontrol strategies.

2.1.2 Larval dispersal and reef connectivity

For all coral groups, larval production was proportional to their areal coverage, and COTS larval production was proportional to the number of adult starfish, increasing by a factor of 4 for each age class and plateauing after 4 years (Pratchett et al. 2014; Babcock et al. 2016). Emperor and grouper larval production per individual doubled for each age-class and increased with latitude due to the temperature sensitivity of larval fish (O'Connor et al. 2007; Pratchett et al. 2017; Barneche et al. 2018). Dispersal following spawning at each reef was modelled by combining: particle tracking techniques based on the OceanParcels code (https://oceanparcels.org); underlying ocean currents from 7 years of simulation (2015–2022) using the eReefs 1 km resolution hydrodynamic model; and the preferred swimming depths, and mortality rate of COTS, coral and fish larvae (Steven et al. 2019; Baird et al. 2021). Particles passing within 1 km of a reef were counted as potentially contributing to recruitment at that reef.

2.1.3 Ecological interactions and responses

Ecological communities represented on each reef included corals, COTS, benthic invertebrates, invertivorous fish, emperors and groupers (**Table 1**). 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 AIMS LTMP. The reef survey data from LTMP included estimated percent coral cover along reef circumferences (manta tows) and fish abundances from underwater visual surveys along fixed transects repeated yearly (Emslie et al. 2020).

Table 1. 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	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		LTMP
Invertivores (triggerfish, cardinal fish)	T	N/A	Site	Natal reef	Benthic invertebrates	Nil
Emperors (redthroat *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)

For the purposes of the model, coral communities were represented by five functional groups: staghorn *Acropora*, tabular *Acropora*, *Montipora*, Poritidae and Merulinidae, distinguished within the model in terms of their growth rates, fecundity, preference by COTS, and susceptibility to environmental impacts such as cyclones and marine heatwaves (Álvarez-Noriega et al. 2016; Tan et al. 2016; DeVantier and Turak 2017). COTS populations were size-structured, differentiating larvae (age 0 years), herbivorous juveniles (age 1 year) and five corallivorous adult classes (ages 2, 3, 4, 5 and 6+ years). Trophic interactions between corals and COTS were calculated using a formulation that included: a delay of the juvenile-to-adult transition with low coral cover (Deaker et al. 2020); increasing adult COTS predation rates with age (Frieler et al. 2013); a preference for faster-growing corals (Pratchett et al. 2020); and onset of senescence from age 6 (Frieler et al. 2013). Rate parameters such as growth, predation and natural mortalities were fitted to LTMP data (Plagányi et al. 2014).

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 cardinalfish), emperors (redthroat and spangled) and groupers (coral trout species). Trophic interactions between these groups are indicated in **Figure 2** and **Table 1**. For age-structured fish groups (emperors and groupers), predation rates increased linearly with age. 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 2**).

2.1.4 COTS Control

Reefs in the model were prioritised for management intervention following the priority list generated by the COTS Control Program. The program was established in 2012 and has used an Integrated Pest Management (IPM) approach since 2018 (Westcott et al. 2016; Fletcher et al. 2020; Matthews et al. 2024). This IPM framework draws upon empirical and modelled data, and consultation with field operators to prioritise reefs for COTS control activities, via a structured decision process for reefs in a local area of control vessel operation (Fletcher et al. 2020). Priority reefs are those that have economic (e.g. as tourism sites) and/or ecological value (e.g. as larval source reefs) and are vulnerable to COTS during any of the stages of the outbreak wave. The final criteria for prioritisation are logistical factors (Matthews et al. 2024). A subset of priority reefs is selected each year which, after consultation, become target reefs for culling. Priority reefs are intensively controlled until an ecological threshold is reached and then maintained by periodic surveillance (Fletcher et al. 2020).

Implementation of COTS control within the CoCoNet model is relatively sophisticated (Castro-Sanguino et al. 2023). Each year, reefs are treated in order of their priority until all available capacity (specified in terms of the number of vessels and divers) has been utilised. The effort required to control each reef site to the COTS density threshold is dependent on the pre-existing COTS density. Once a site has been controlled, it continues to be monitored and controlled as long as the control program continues to operate. For all scenarios described here, control only begins in 2026.

2.1.5 Fisheries

The model included catches of both emperors (redthroat and spangled) and groupers (coral trout). Commercial and charter catches recorded from 1989 to 2021 and supplied by the Queensland Department of Primary Industries (QLD DPI) 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) (Northrop and Campbell 2020). Catch rates were assumed to be zero for fish under 3-years of age and equal for all ages from 3-years. Several fisheries management changes influenced catch rates over the time period in which QLD DPI data was collected. These included a growing shift to live reef finfish trade focused on coral trout (*Plectropomus* spp.) from around 1996 (Mapstone et al. 2001); further restricted fish size limits (coral trout: 1996; redthroat emperor: 2003); and major changes in 2003–2004, including limitations and changes to commercial licences, restructure of the commercial line fishing fleet (buy-back), introduction of individual transferable quotas, altered reef fish possession limits, gear restrictions, and seasonal (spawning) fishing closures (Northrop and Campbell 2020). GBRMP Zoning regulations were applied in the model from 1987, with more than 1,000 reefs declared as no-take zones (fishing prohibited) as part of the 2004 rezoning (Day 2008). It was assumed that all fishing (reported and unreported) occurred in the remaining open-to-fishing zones. Assumptions include 100% compliance in green zones (no-take zones closed to fishing) and 100% compliance to all other fisheries management regulations (e.g. fish size limits, possession limits).

2.2 Model calibration

CoCoNet has been calibrated in the past against the LTMP dataset (Sweatman et al. 2011) at both the individual reef scale (Plagányi 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 coral recovery at close to their observed periodicity (Condie et al. 2018). The current project required recalibration of the model to include comparison of emperors and groupers with LTMP data at regional scale. The recalibration process included a mix of formal parameter estimation and heuristic parameter search to fine-tune the model, ensuring improved alignment with LTMP data.

2.3 Scenario development

The hypothetical scenarios (referred to as 'management scenarios' throughout) developed for testing were chosen for their relevance to the protection of fish species that are likely to either prey directly on COTS or influence COTS predators indirectly through the food web (**Table 2**). We also considered direct COTS control efforts in the form of the number of COTS control vessels (currently 5–6), to understand the relative and/or combined benefits that might be achieved by predator biocontrol (i.e. protection or augmentation) and direct culling through the COTS Control Program.

Table 2. List of potential management scenarios chosen for testing with CoCoNet. Scenario 0 precluded any management intervention for the entire historical and forecast period of 1956–2050. Scenario 1 deployed historical management arrangements over the period 1956–2024, with 2024 management retained through to 2050. Scenarios A–L were identical to Scenario 1 for the period 1956–2025, then adopted distinct management scenarios for the period 2026–2050. Note that percentages of reefs are based on current reef definitions and therefore may differ from historical descriptions.

Scenario	Name	Description	Type of management scenario
0	No management	No management restrictions applied historically or in the future.	None
1	Historical management	~4% no-take zones from 1987, increasing to ~30% from 2004 with additional fisheries restrictions (see Section 2.1.5).	Marine Protected Area and fisheries management
A	5 Control vessels	5 COTS control vessels operating on reefs selected by GBRMP prioritisation.	Manual control
B	10 Control vessels	10 COTS control vessels operating on reefs selected by GBRMP prioritisation.	Manual control
C	40% Green zones	No-take zones increased to 40% of all reefs.	Marine Protected Area management
D	60% Green zones	No-take zones increased to 60% of all reefs.	Marine Protected Area management
E	100% Green zones	No-take zones increased to 100% of all reefs.	Marine Protected Area management
F	50% catch reduction	Total catch of emperors and groupers reduced to 50% of historical levels.	Fisheries management
G	Emperor stock boost	Annual release of 2,000 juvenile emperors on all 500 GBRMP priority reefs.	Augmentation

Scenario	Name	Description	Type of management scenario
H	No fishing on outbreaking reefs	Fishing closures on reefs with COTS outbreaks	Fisheries management
I	Upper size restriction on emperor catches	Catch of largest size class fish (≥ 5 yo) reduced to zero.	Fisheries management
J	Lower size restriction on emperor catches	Catch of smallest size class fish (≤ 3 yo) reduced to zero.	Fisheries management
K	A + E	5 control vessels + 40% Green zones	Marine Protected Area plus manual control
L	B + C	10 control vessels + 100% Green zones	Marine Protected Area plus manual control

Each model run started in 1956 to allow the system to equilibrate, before new management interventions were introduced from 2026 and then run through to 2050. Every scenario was rerun 20 times, with the timing and magnitude of events such as cyclones, heatwaves and COTS spawning based on historical information or varying stochastically between runs. This 20-member ensemble of runs thereby captured the range of uncertainty associated with future projections.

2.4 Stakeholder engagement

The Reef Authority, QLD DPI and the Great Barrier Reef Foundation (GBRF) were consulted to ascertain their priorities for testing model scenarios (Appendix A). These included adjusting the number of no-take zones, COTS Control Program effort (number of vessels), fishery size and take limits, and the stocking of juvenile emperors. Top ranking scenarios were prioritised for model development.

2.5 Hindcasting scenarios

Hindcasting was designed to understand the potential biocontrol benefits of the 2004 rezoning of the GBR along with associated changes in fisheries management. The first "counterfactual" scenario was one in which no zoning or fisheries management took place (Scenario 0). Scenario 1 mimicked the GBR management history, with ~4% no-take zones implemented in 1987, and a major rezoning implemented in 2004, whereby ~30% of the GBR reefs were assigned a no-take status[1], with additional changes in fisheries management. Four emergent response variables from CoCoNet were explored: 1) proportion of reefs with COTS outbreaks (> 15 adult COTS ha^{-1}); 2) total hard coral cover (%); 3) emperor density (ha^{-1}); and 4) grouper density (ha^{-1}). Analysis focused on the period 2004–

[1] The percentage of no-take zones depends on how reefs are demarcated. When they were first declared, the number of identified individual reefs was fewer and the associated higher percentages (4.5% and 33%) continue to be widely used in the literature.

2022, during which the two scenario trajectories diverged due to the influence of zoning and fisheries management in Scenario 1.

Scenarios were compared in three ways. Firstly, for response variables in each of the 20 runs in the ensemble, we compared the ratio between the counterfactual (Scenario 0) and the historical management scenario (Scenario 1). Specifically, for each scenario, run, year and response variable, we calculated an average across all reefs in the GBRMP, and then calculated the ratio between the two scenarios. Secondly, we calculated the ratio between no take zone and fished zone reefs for each scenario, run and variable in each of ten latitudinal sectors on the GBR in 2004 and 2022. Third, we compared the average no-take-to-fished-zone ratio within 2004–2022 at the regional (North, Central, South) level. These were compared to averages calculated from the AIMS LTMP data including: the proportion of survey reefs with COTS outbreaks and percent coral cover per reef estimated from manta tow surveys, and fish densities calculated from transect data along permanently marked sites. It is important to note that the number of reefs surveyed by the LTMP varied among years, and that CoCoNet yields emergent responses at the reef level. Quantities of COTS and coral cover can only be directly compared using data from manta tow surveys which are conducted around entire reef perimeters. Fish monitoring along permanently marked transects only occurs in a single standardised reef slope habitat at each reef, generally the north-east flank. However, it is currently the only available dataset at the desired spatio-temporal scale to yield a reasonable comparison to CoCoNet simulations of reef fish dynamics. Some reefs were excluded from the regional comparison (3.5% of the 3,806 reefs, translating to 3,653 reefs included) because they fell outside the geographical coordinates of the bounding polygons.

2.6 Forecasting scenarios

Forecasting was generated under a series of scenarios (**Table 2**), all with distinct management scenarios (Scenarios A–L) starting in 2026 and ending in 2050. Prior to 2026, all management scenarios were identical to the historical management scenario (Scenario 1). We evaluated the same four emergent response variables from our hindcasting analysis (see above). For each of the 20 runs in the ensemble and each of the response variables, we calculated the difference between Scenario 1 and the management scenario (Scenarios A–L) at the whole-GBR level (rather than the ratio used for the hindcast). We then compared these differences across scenarios in 2035 and 2045 to identify effects of 10-years and 20-years of management intervention. Two combinations of management interventions were also run, one highly plausible (Scenario K) and one extremely ambitious (Scenario L) with the results presented in Appendix B.

Australian Government Reef Trust | Great Barrier Reef Foundation | Australian Government Australian Institute of Marine Science | CSIRO | James Cook University Australia | The University of Queensland Australia

3. RESULTS

3.1 Hindcast modelling

The hindcast modelling estimated that by 2024 the effect of GBRMP Zoning and additional fisheries restrictions enacted over the period 1987–2004 was a 70% relative reduction (not to be confused with an absolute reduction[2]) in the median number of reefs with COTS outbreaks (95% highest density continuous interval, H.D.I.: 47–86%) and a 13% relative increase in GBR-wide median coral cover (95% H.D.I.: -7–54%) compared with the counterfactual scenario of no zoning or fisheries management (**Figure 3**). The modelling estimated substantial gains in the densities of emperors (median: 15,193%; 95% H.D.I.: 7,138–26,866%) and groupers (median: 4,334%; 95% H.D.I.: 1,925–7,563%) as a result of historical management interventions that the model suggests prevented the collapse of these stocks. The absolute changes in these populations attributed to GBRMP management in 2025 and 2050 are shown in **Figure 4**.

[2] For example, if in 2022 the counterfactual scenario (Scenario 0) had 16% of all reefs under a COTS outbreak, whereas the historical management scenario (Scenario 1) had 3.2%, the ratio would be 3.2/16 = 0.2 (i.e. (1 – 0.2) * 100, approximately 80% relative reduction), whereas the absolute difference would be 3.2-16 = -12.8% outbreaking reefs.

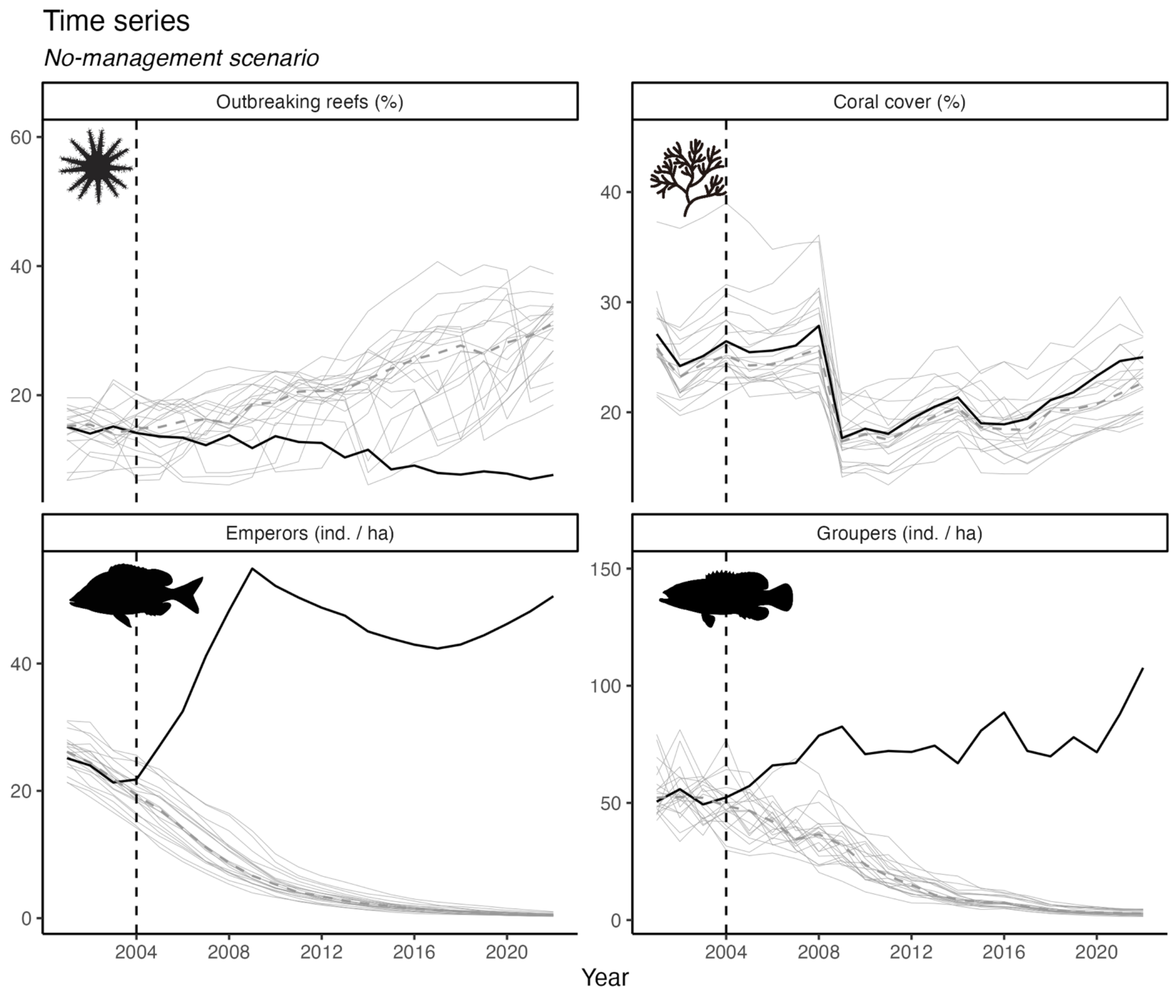

Figure 3. Model results comparing the effects of historical zoning and fisheries management (Scenario 1) to the hypothetical no management counterfactual (Scenario 0) for the four response variables. Black solid line is the median trend for Scenario 1, dashed grey line is the median trend for Scenario 0, and grey lines are individual runs from Scenario 0.

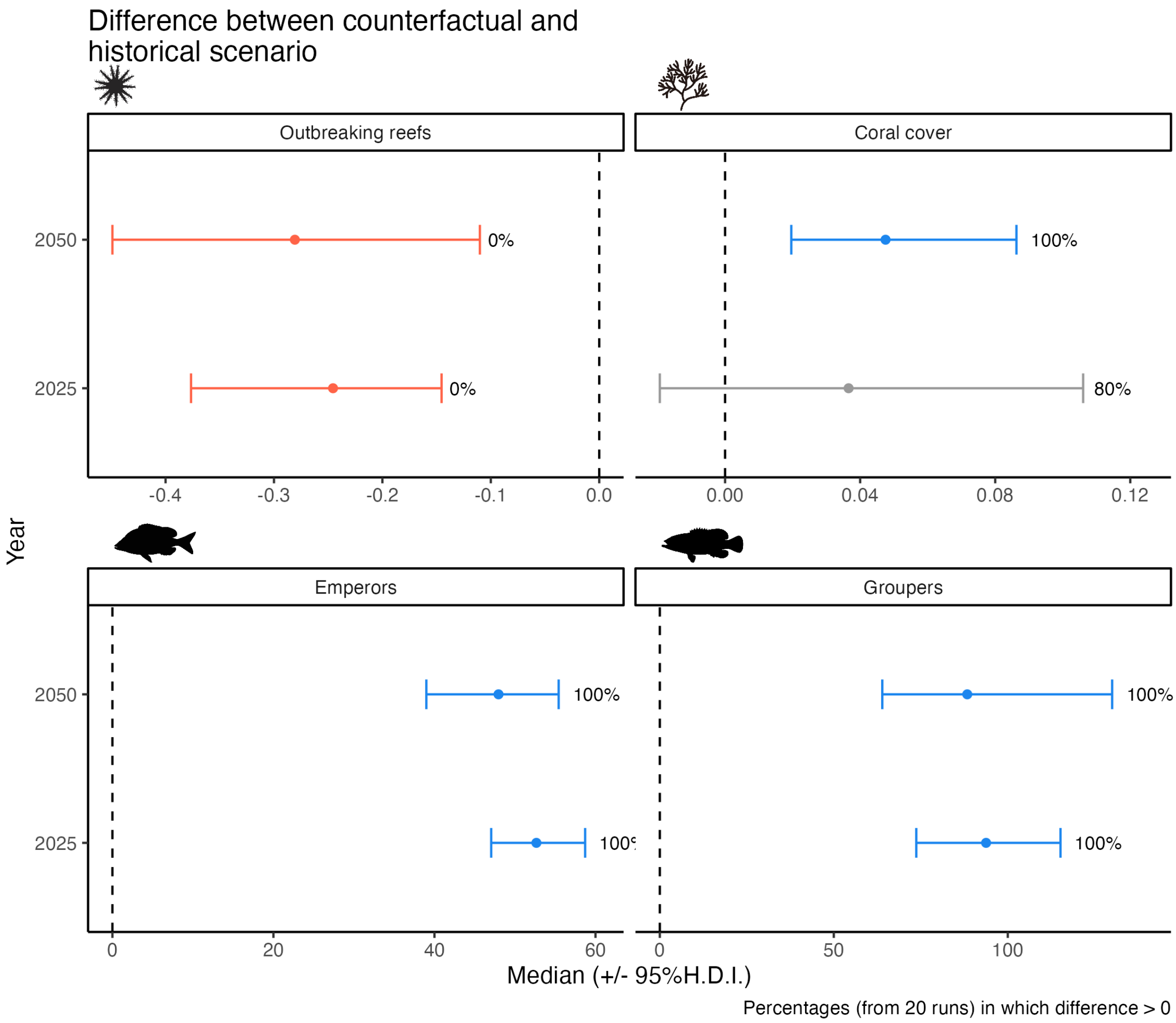

Figure 4. Differences between historical zoning and fisheries management (Scenario 1) and the hypothetical no management counterfactual (Scenario 0) in 2025 and 2050. The median (circle) and the 95% H.D.I. across ensemble-level differences are presented, as well as the percentage of runs in which the difference was above 0. Red colour shows 95% H.D.I. fully below 0, blue is fully above 0. The 2025 results indicate that historical management has provided substantial reductions in the fraction of reefs with COTS outbreaks (represented by bars (95% H.D.I.) positioned fully to the left of the zero dashed line and coloured red); some gains in fractional coral cover (represented by bars crossing the zero line and coloured grey); and substantial gains in emperor and grouper densities per ha (represented by bars fully to the right and coloured blue). The 2050 results are similar, except that gains in coral became more substantial (represented by bars fully to the right of the zero line and coloured blue).

Hindcast modelling indicated that the proportion of reefs under COTS outbreaks in no-take zones compared to fished zones decreased in all sectors (i.e. the ratios became lower) between 2004 and 2022 as the management interventions took effect (**Figure 5**). Coral cover became relatively higher in no-take zones in all sectors except those in the far north (Cape Grenville and Princess Charlotte Bay) and far south (Capricorn-Bunker). The largest increases were in the Cairns and Innisfail sectors. The ratio for emperors was marginally higher in most sectors, but lower in the Cairns and Innisfail sectors. The ratio for groupers was larger in all sectors except Cooktown-Lizard and Cairns, where it decreased slightly from 2004 to 2022. By 2022, Cooktown-Lizard was the only sector that had higher fish abundance (groupers) in fished zones than no-take zones (ratio above 1). These results suggest that the management actions implemented throughout the GBR's history were effective, in that the model resulted in more emperors and groupers observed in no-take zones in most regions, with flow-on effects for COTS outbreaks and coral cover. It is important to note, however, that when examining how the average no-take-to-fished-zone ratios (2004–2022) compared between CoCoNet's Scenario 1 and LTMP monitoring data (254 reefs) by GBR region (e.g. northern, central, southern), there was 50% alignment across factors and regions (i.e. 9 of 12 plots show both sources above or below the line together; Appendix C). It is likely that the difference between the numbers of reefs in the two datasets has affected the results, and they therefore need to be interpreted with caution.

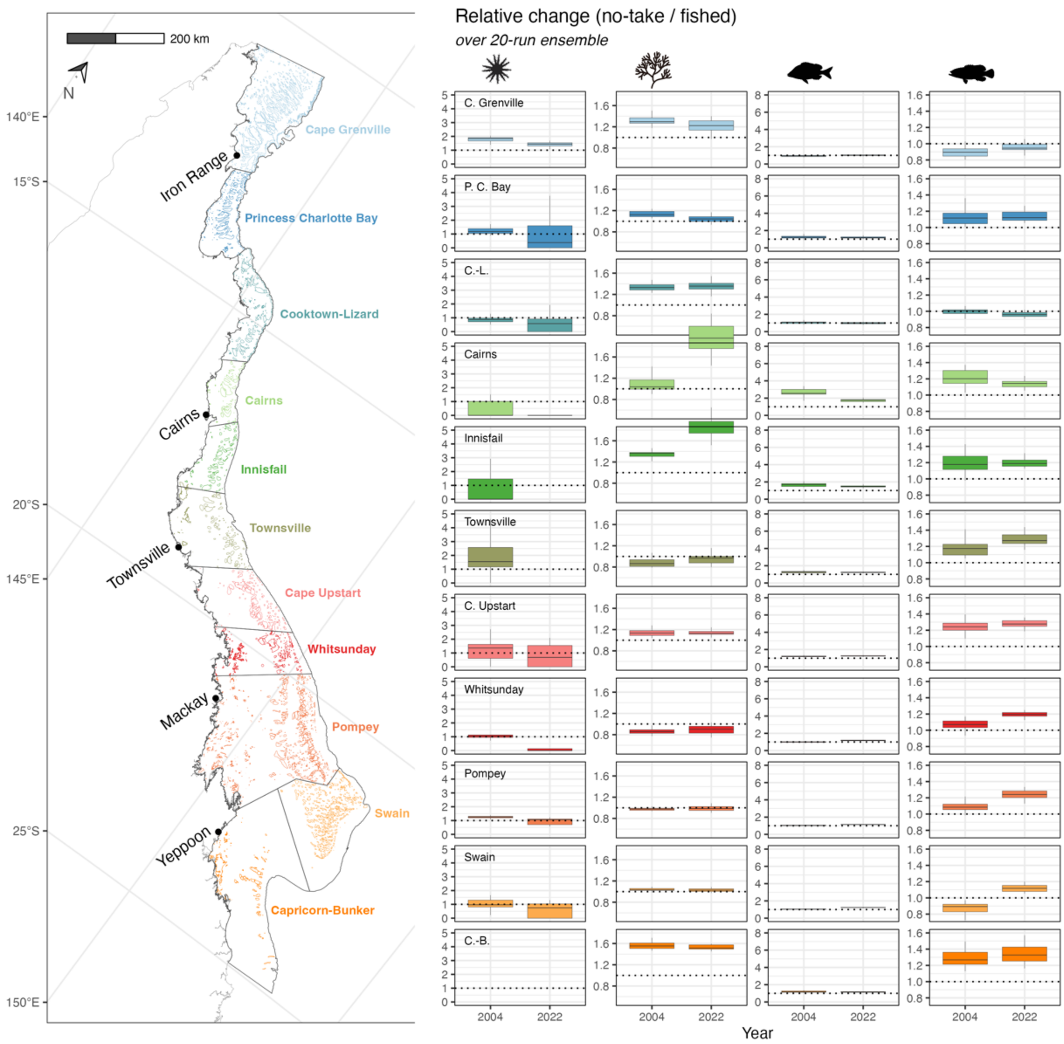

Figure 5. Model results comparing how the ratio between no-take and fished zones have changed over time (2004 and 2022) under the historical management scenario (rezoning to ~30% no-take, fisheries management regulations, Scenario 1), partitioned by latitudinal sectors of the GBR (3,806 reefs). Each boxplot conveys the median ratio (central line), followed by the 25th and 75th percentiles (the lower and upper hinges). The upper/lower whiskers extend from each hinge to the largest/lowest value no further than 1.5 x IQR (inter-quartile range) from the hinge. Plot columns, from left to right, comprise the: proportion of COTS outbreaking reefs, coral

cover, emperor density and grouper density. Dotted horizontal line indicates equal numbers of each variable in no-take zones and those open to fishing.

3.2 Forecast modelling

Twelve management scenarios (Scenarios A–L) were chosen for modelling from 2026 to simulate their potential effect on COTS outbreaking reefs (as a proportion of the 3,806 reefs), coral cover (percentage), and numbers of emperors and groupers (individuals per hectare). Scenarios included: 5 or 10 COTS control vessels; no-take zones covering 40%, 60% and 100% of the GBRMP; 50% reduction in catch; a yearly boost of juveniles to emperor stocks on priority reefs; fishing excluded from reefs with outbreaks; minimum and maximum emperor size limits; and 2 combination scenarios (**Table 2**). We assessed the modelled benefit of these scenarios compared to the historical conditions (Scenario 1) through to 2050, with the goal to reduce COTS outbreaks and increase coral cover.

Historical zoning and fisheries management were predicted to continue to contribute to the suppression of acute COTS outbreaks and the maintenance of emperor and grouper populations, against a background of coral cover benefits being eroded by climate change impacts (**Figure 6**). Individual trajectories exhibited high variability through time, with large differences between trajectories. However, median trajectories suggest that the benefits of historical management had been largely realised by the mid-2020s (**Figure 6**).

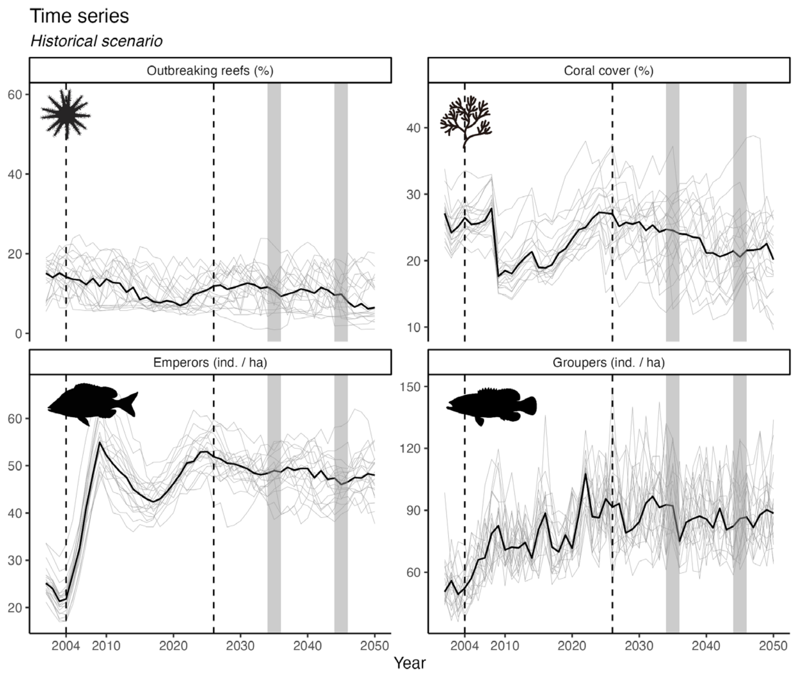

Figure 6. Forecast model trends through time among the four response variables for the historical management scenario (Scenario 1). Solid line indicates median trends, and grey lines indicate individual model runs. Vertical dashed lines at 2004 and 2026 indicate implementation of the rezoning and manifestation of future alternative interventions (started in 2025), respectively. Grey vertical bars in 2035 and 2045 visually highlight the trends of Scenario 1 at 10 and 20 years post alternative interventions.

Model scenarios mostly produced beneficial effects in median trends of the response variables (**Figure 7**), although effects were often small relative to variations amongst individual runs within the ensembles (**Figure 8**, **Figure 9**, **Figure 10**, **Figure 11**). Active removal of COTS by 5 and 10 COTS control vessels (Scenarios A and B) was most consistent in reducing the median number of reefs with COTS outbreaks (up to 36% reduction by 2050), while reducing catches by 50% and 100% no-take zones across the entire GBRMP (Scenarios F and E) were most effective in increasing the median densities of emperors and groupers (up to a 14% increase by 2050) (**Figure 7**). The most effective strategies for increasing coral cover were increases in no-take reefs to 40% (Scenario C) or fishing excluded from reefs with outbreaks (Scenario H) with up to an 8% increase by 2050 for both scenarios (19% decrease to 45% increase across ensemble runs), whereas 100% no-take (Scenario E) and 5 COTS control vessels (Scenario A) yielded increases of approximately 2% (19% decrease to 32% increase across ensemble runs) by 2050 (**Figure 7**). Interestingly, no additional benefits were derived by combining interventions (Scenarios K and L, Appendix D).

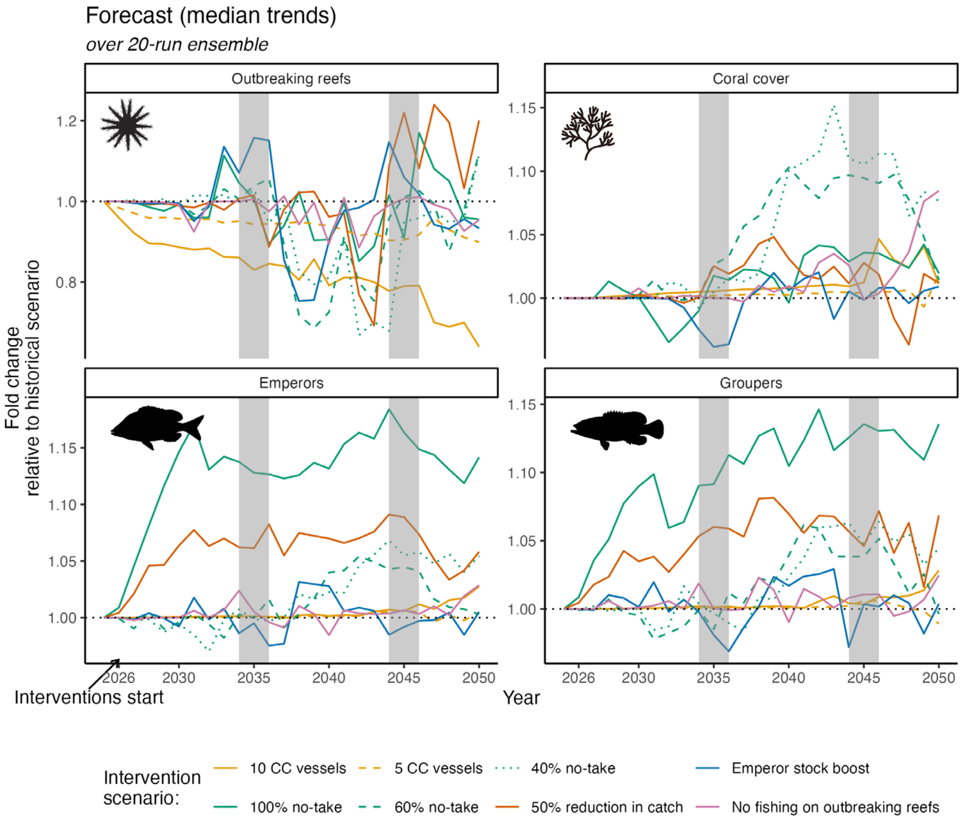

Figure 7. Model results comparing the fold change in median trends in hypothetical management scenarios (starting at 2026) relative to the historical management scenario (CC vessels refer to COTS Control Program vessels). Trends have been smoothed using a 6-yr moving average window. Y axes represent fold change (i.e.

management scenario divided by historical management scenario) for proportion of reefs with outbreaks, percentage coral cover, and number of fish (emperors and groupers) per ha.

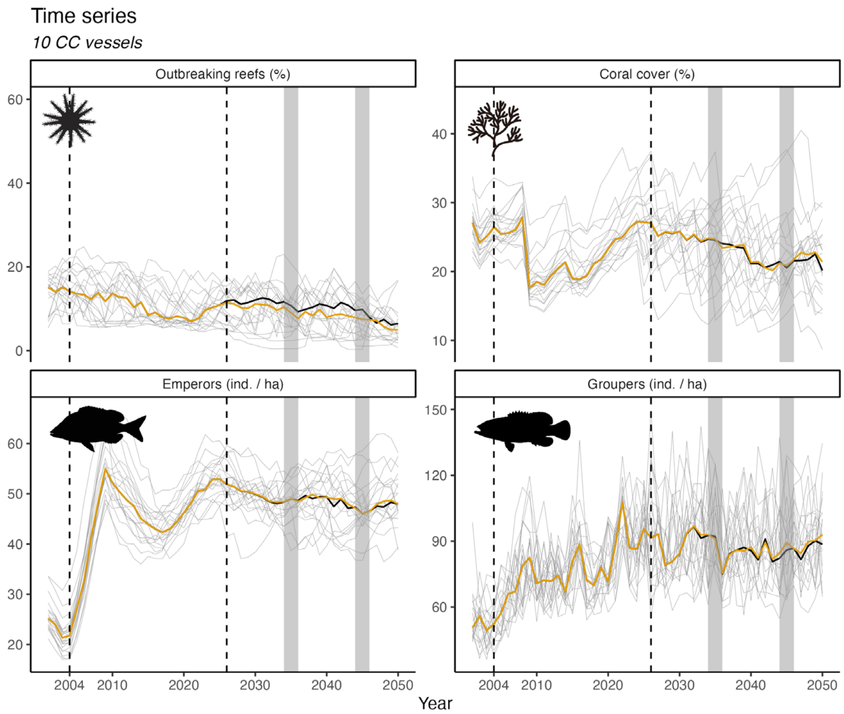

Figure 8. Forecast model trends through time among the four response variables for the 10 COTS Control vessels scenario (Scenario B). Solid lines indicate median trends: coloured line is Scenario B, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario B.

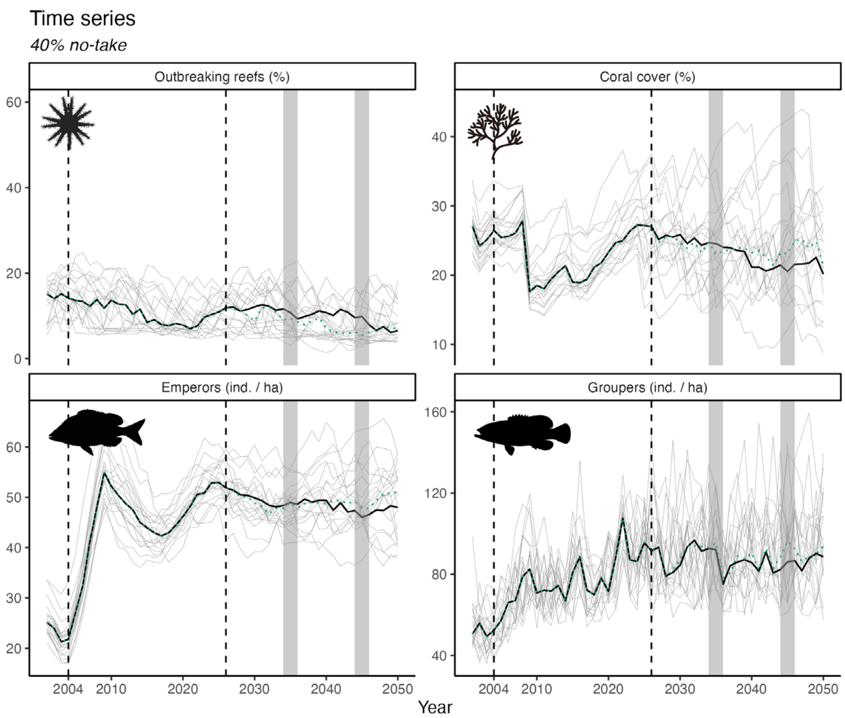

Figure 9. Forecast model trends through time among the four response variables for the 40% no-take scenario (Scenario C). Solid lines indicate median trends: coloured line is Scenario C, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario C.

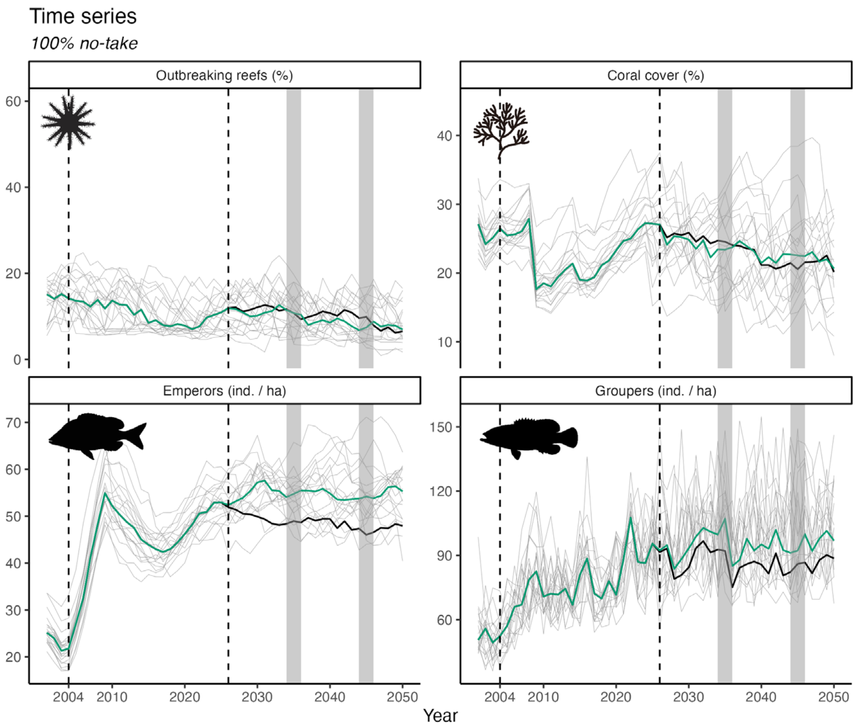

Figure 10. Forecast model trends through time among the four response variables for the 100% no-take scenario (Scenario E). Solid lines indicate median trends: coloured line is Scenario E, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario E.

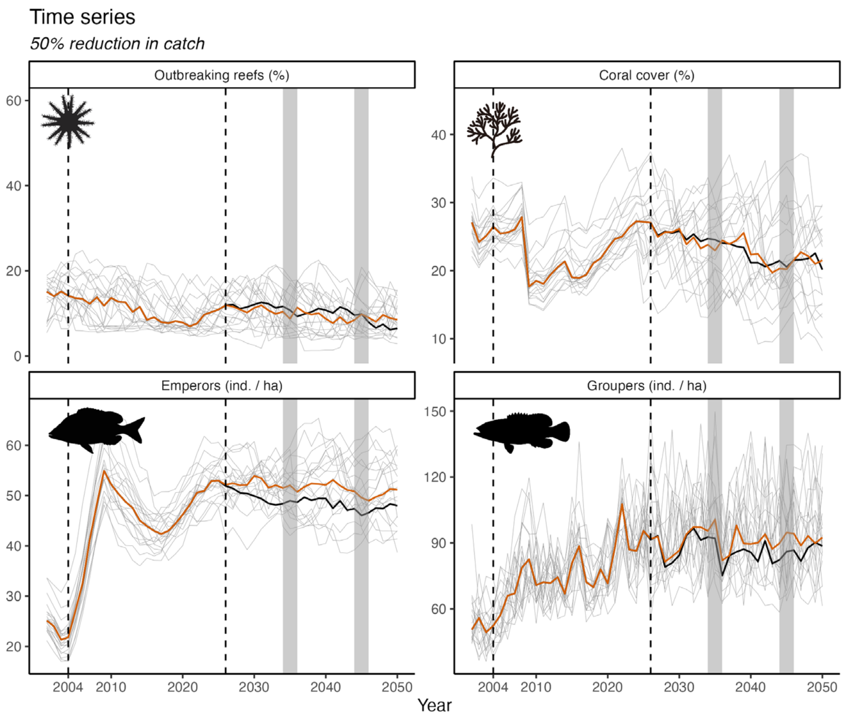

Figure 11. Forecast model trends through time among the four response variables for the 50% reduction in fishing scenario (Scenario F). Solid lines indicate median trends: coloured line is Scenario F, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario F.

Comparisons of the relative median difference in proportion of coral cover for each scenario with the historical management scenario resulted in uncertainty intervals (95% H.D.I.) overlapping zero, indicating that when accounting for the variability among model runs, no substantial benefit was evident after 10-years of intervention (2035, **Figure 12**) or 20-years of intervention (2045, **Figure 13**). In terms of reduced proportions of reefs with COTS outbreaks, the only scenario to provide substantial benefits was deployment of 10 control vessels (**Figure 12**) and even this was subsumed by the underlying variability within 20-years (**Figure 13**). Fish gained substantial benefits from the 100% no-take strategy, with emperors mainly benefiting in the first decade (**Figure 13**) and groupers in the second decade (**Figure 13**). Combining the 100% no-take strategy with 10 control vessels (Scenario L) extended substantial benefits to emperors out to at least 2045, but delivered no other substantial benefits (Appendix D).

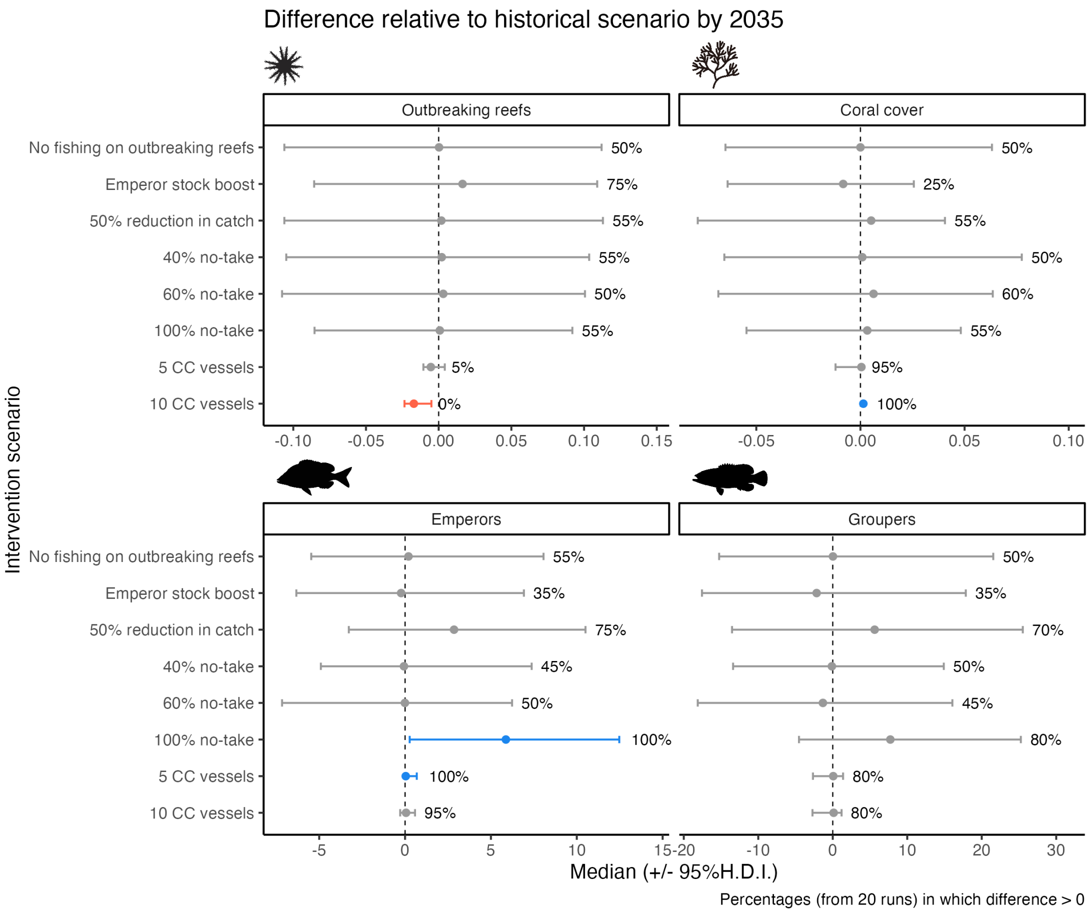

Figure 12. Differences between each scenario and the historical management scenario (Scenario 1) at the ensemble level in 2035. The median (circle, equivalent to the separation of the black and coloured lines within the 2035 grey bar in the time series depicted in Figures 8–11) and the 95% H.D.I. across ensemble-level differences are presented, as well as the percentage of runs in which the difference was above 0. Red colour signifies 95% H.D.I. fully below 0, blue is fully above 0. The forecast of an ideal management scenario when compared to the

historical management scenario would indicate (i) substantial reductions in COTS outbreaking reefs with the bars (95% H.D.I.) positioned fully to the left of the zero dashed line and coloured red, and (ii) substantial gains in median coral cover, represented by bars positioned fully to the right and coloured blue.

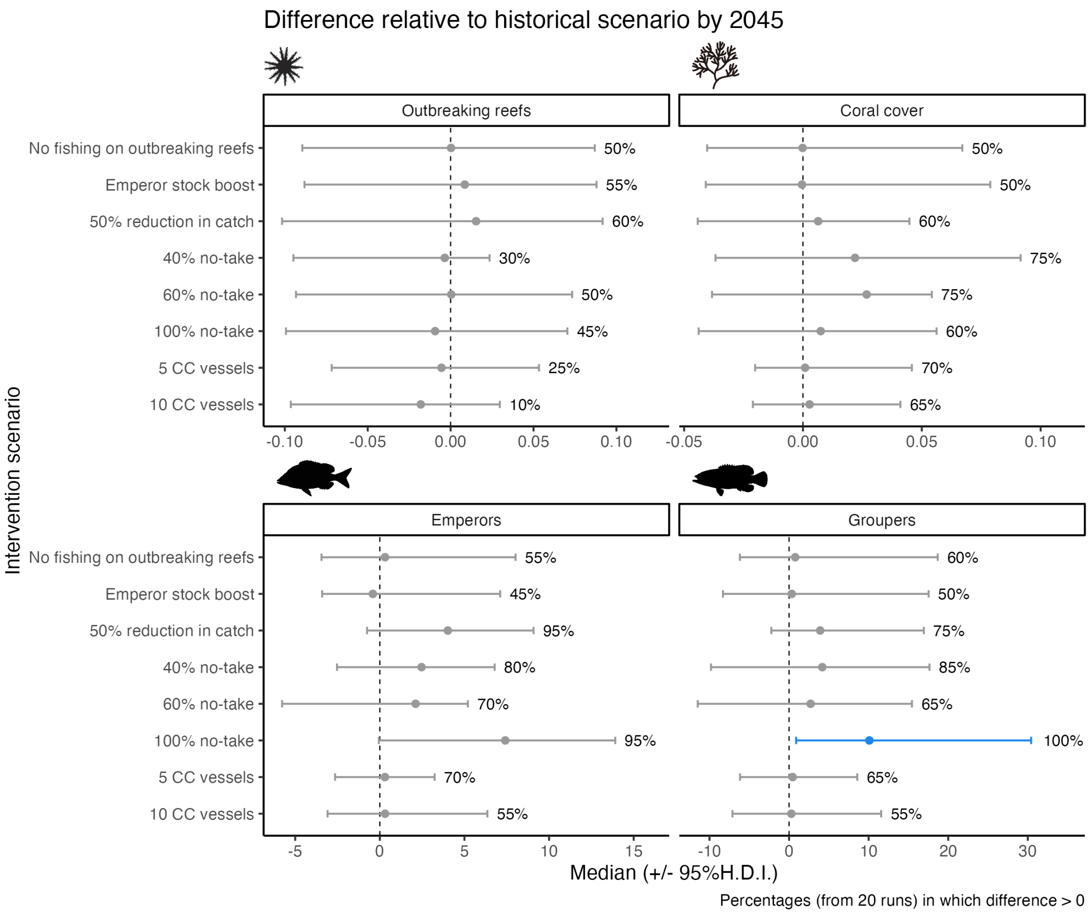

Figure 13. Differences between each scenario and the historical management scenario (Scenario 1) at the ensemble level in 2045. The median (circle, equivalent to the separation of the black and coloured lines within the 2045 grey bar in the time series depicted in Figures 8–11) and the 95% H.D.I. across ensemble-level differences are presented, as well as the percentage of runs in which the difference was above 0. Red colour shows 95% H.D.I. fully below 0, blue is fully above 0. The forecast of an ideal management scenario when compared to the historical management scenario would indicate (i) substantial reductions in COTS outbreaking reefs with the bars (95% H.D.I.) positioned fully to the left of the zero dashed line and coloured red, and (ii) substantial gains in median coral cover, represented by bars positioned fully to the right and coloured blue.

4. DISCUSSION AND OUTPUTS

This study is the first to use a modelling approach to hindcast and forecast scenarios designed to enhance the populations of fish that affect COTS through the food web as a biocontrol measure. Our results are underpinned by the hypothesis that an intact fish assemblage buffers reef health and resilience. On the GBR, this is in part achieved by protecting fish predators of COTS through zoning and fisheries management, which in turn helps sustain coral cover. The models suggest that protection of a significant portion of reefs within the GBRMP as no-take zones, combined with greater fisheries restrictions, has contributed to the ‘protect fish—reduce COTS—protect coral’ biocontrol pathway. Modelling scenarios to increase these protection measures in various ways offered a low-risk method of testing options that would be economically, socially and culturally difficult in the real world. Hindcasting existing management measures against a ‘no management’ counterfactual revealed that the zoning and fisheries management measures currently in place have contributed to reductions in COTS outbreaks and gains in coral cover over the past 20 years. The outcomes of modelling for increased zoning and COTS control showed some benefits in reducing COTS outbreaks and increasing coral cover, albeit with very high variability in the modelled magnitudes of these effects. Many of the modelled scenarios, including zoning changes, fisheries management and stock augmentation showed potential benefits to the fish groups, but diminishing returns for COTS outbreak reduction and coral cover gains. This was especially evident when forecasting scenarios to 2050, where projected changes in climate tend to overwhelm much of the benefit expected from any of the modelled management changes over the next 25 years.

4.1 Hindcast modelling: fish conservation as biocontrol

Our novel approach to assessing the efficacy of fish predator conservation or enhancement as a method for COTS biocontrol indicates 20 years of benefits from the 2004 rezoning plan and fisheries management actions. Our hindcast models show increased emperor and grouper numbers, a decline in the number of reefs under COTS outbreaks, and increased coral cover due to these measures. This result supports the ‘predator removal hypothesis’ (both direct and indirect effects) as an important factor in understanding the health of the GBR over the past 50 years. Since the 2000s, evidence suggests that no-take zones have been associated with a reduction in COTS outbreaks (Sweatman 2008), and although a small field trial to measure actual fish predation rates on juvenile starfish was inconclusive (Sweatman 1995), the direct relationship between the removal of fish biomass by fisheries and COTS outbreaks has since been demonstrated (Kroon et al. 2021). Our hindcast modelling confirms that the protection of predatory reef fishes has contributed to mitigating coral loss from COTS outbreaks. While the magnitude of these effects varied spatially across the GBR, they were detectable at the whole-GBR scale. While the management measures imposed in 2004 were not implemented with a view towards biocontrol, our results, together with global literature, suggest that this inadvertent outcome is effective.

Other studies have used modelling techniques to simulate the effect of COTS outbreaks and various interacting factors and threats, including fishing. Milne et al. (2023) used a spatially explicit model to predict the severity of COTS outbreaks in the Philippines and Saudi Arabia, along with the effects of several management strategies. The model included herbivorous fish as the only group of fishes, but despite the lack of a direct trophic link, they demonstrated that overharvesting herbivorous fish significantly affected COTS and coral populations. Negative associations between COTS outbreaks and fish size were also detected in the Northern Mariana Islands (Houk et al. 2014). A model of intermediate complexity for ecosystem assessments (MICE) to compare scenarios including fish predation, but excluding fishery mortality of the fish, found that even high levels of fish predation did little to reduce adult COTS numbers, while invertebrate predation on juvenile COTS was more effective (Morello et al. 2014). CoCoNet includes this same pathway: within the model, groupers prey upon invertivorous fish (e.g. triggerfish), which in turn prey on benthic invertebrates (e.g. decorator crabs), which consume juvenile COTS, although there are still high levels of uncertainty in predation rates at each step. Additionally, groupers are known to consume small planktivores such as damselfishes, which in turn are likely to prey on COTS larvae (Kroon et al. 2020). We acknowledge the early stages in our understanding of all the trophic pathways considered here, having been detected through eDNA, field or lab observations. Harnessing and re-parameterising CoCoNet for the purposes of exploring biocontrol scenarios has offered a new and more powerful modelling option, with the additional benefit of empirical data (e.g. LTMP monitoring data) against which it can be calibrated.

Explaining the smaller-scale spatial patterns throughout the GBR will undoubtedly require a more targeted investigation of relationships between COTS and fishing pressure gradients (Dulvy et al. 2004). Research elsewhere indicates mixed responses of COTS densities to fishing. Outbreak-level COTS densities on isolated atolls in the Chagos Archipelago, where fishing is extremely limited (Roche et al. 2015), lends support to the idea that changing only one or two aspects of this highly complex socio-ecological system may not produce a clear and predictable response. Clements and Hay (2017) offer an interesting perspective from a Fijian study on very small marine protected areas (MPAs): because MPAs had higher coral cover, COTS were attracted to these areas, resulting in higher COTS densities inside the MPAs. Evidence for partial predation that injured starfish in the Philippines was linked to no-take areas (Rivera-Posada et al. 2014), and was also higher within GBR no-take zones compared to other zones where fishing is permitted (Caballes et al. 2022), although an earlier GBR study had detected no effect of zoning (Messmer et al. 2017). While injuries may not result in mortality, it can be hypothesised that a reduction of COTS resources for fecundity could result from redirection of energy to tissue repair (Pratchett et al. 2017).

4.2 Efficacy of intervention options

Our modelling results indicated that deployment of 10 COTS control vessels will likely result in greater reductions in COTS outbreaks than expansion of predator conservation measures alone. We included COTS control efforts as potential scenarios to offer realistic options and acknowledge that in the context of protecting reefs from COTS, biocontrol measures need to be considered in tandem with more direct methods of COTS reduction. The current COTS Control Program has undertaken surveillance and targeted culling of COTS at hundreds of reefs within the GBR Marine Park since 2012, with 5–7 vessels in operation since 2018 (Matthews et al. 2024). Our modelled management scenarios suggest that expansion of the COTS Control fleet to 10 vessels will likely decrease the median number of outbreaking reefs, with the potential for modest increases in coral cover (**Figure 7**). Additional COTS control effort is likely the most achievable option to implement, given the high socio-economic costs involved in changing current zoning and fisheries management (Day 2022).

Increasing the number of no-take zones to 40% or stopping fishing on outbreaking reefs were the most effective strategies in increasing coral cover by 2050, although the level of temporal variability was high. Interestingly, although increasing no-take zones to 60% provided the most rapid response, by the mid-2040s it was the modest increase (40% no-take) that provided the greatest benefit with mean GBR coral cover enhanced by around 10% (**Figure 7**). Hence, changing the protection status of a few hundred reefs to no-take may deliver a substantial benefit. The reason that a modest number of no-take zones may be more effective than a larger number is presumably because fishing is being displaced to other reefs by this process, rather than being removed. In any case, it should be emphasised that this analysis is based only on median values and there are large uncertainties associated with predicted benefits (**Figure 13**). Furthermore, altering spatial management within the Marine Park is a complex, contentious and challenging task (Day 2022) with subsequent flow on effects to multiple users. Cost-benefit analyses for any of the intervention options will need to account for these complexities, as well as the underlying uncertainties in ecological responses.

Not surprisingly, fish benefited most from reductions in fishing (**Figure 7**). This included complete removal of fishing through declaration of 100% no-take zones, which was the only strategy that provided a substantial increase in emperors (**Figure 12**) and groupers (**Figure 13**). By 2050, increasing no-take zones to 40% provided similar benefit to imposing a 50% reduction in fishing across the GBR. In practice, emperors and groupers exhibit varied responses to fishing pressure and management strategies (Mapstone et al. 2004), in part due to regional variation in growth and reproductive biology (Adams et al. 2000; Williams et al. 2006; Currey et al. 2013; Carter et al. 2014). It may also take many years for potential benefits of no-take areas on groupers and emperors to eventuate (Mapstone et al. 2004), and therefore we may need to take a time lag into account for the changes in fish populations to affect COTS outbreaks and coral cover.

4.3 Factors limiting the benefits of intervention

There are multiple factors limiting the benefits that can be achieved through any reef intervention. While hindcast modelling benefits from comparisons with empirical data, forecast modelling is undertaken within the context of increasing uncertainty of a changing climate. All scenarios reported here were conducted under the IPCC's SSP1–2.6 projection (1.8ºC average temperature increase by 2100) (IPCC 2021). While this projection is now considered to be conservative, benefits under nearly all interventions plateaued by the 2040s and many started to decline. More extreme climate projections have been shown to negate other types of intervention (Condie et al. 2021).

Another factor that may limit the effectiveness of zoning strategies is the "squeeze effect" whereby fisheries catches are displaced to neighbouring reefs rather than being removed from the system. Groupers are most likely to be susceptible due to their exposure to higher fishing pressure (GBR total catch: 1,027 tonnes per year coral trout compared to 253 tonnes for redthroat emperor (Campbell and Northrop 2020; Northrop and Campbell 2020)). After implementation of the 2004 rezoning plan, higher density fishing locations occurred for commercial, charter and recreational fishers displaced from previously fished areas that became no-take (Lédée et al. 2012; De Freitas et al. 2013), contributing to the dissatisfaction of fishers at the time. While there was no evidence either in the model or in reality that this change impacted fish abundances in fished zones following the 2004 rezoning (Emslie et al. 2015), it does appear to have influenced future scenarios involving increased no-take zones. For example, total fish abundances initially decreased as total reductions on remaining fished reefs outweighed total increases on new no-take reefs. One consequence was that 40% no-take zones tended to outperform 60% no-take zones in the protection of fish stocks. There is clearly a point where the proportion of no-take reefs is so high that the benefits to them dominate, as illustrated by the high efficacy of the 100% no-take scenario where no displacement of fishing is possible.

A third factor limiting the potential effectiveness of fishing and zoning interventions is the reliance on trophic cascades to limit COTS and benefit corals. While reduced fishing provided immediate benefit to fish stocks, COTS reductions and coral increases only started to emerge after a decade, prior to which median coral cover actually declined slightly (**Figure** 7). The potential for coral to initially decline, even though there might fewer COTS outbreaks, is common to most of the scenarios (**Figure 12**) and can be attributed to changing outbreak dynamics in the model. Specifically, suppressing the magnitude of outbreak peaks, reduces the chance of catastrophic collapse of COTS populations due to over-grazing of coral. As a result, both peaks and troughs of outbreaks became less extreme, thereby lessening predation pressure during the peak of the outbreak and increasing predation pressure between outbreaks. The long-term effect of this change on coral cover depends on the balance of losses and gains over the outbreak cycle and can therefore be net positive or net negative. These results underline the importance of representing complete outbreak cycles across a large number of ensemble runs.

4.4 Model limitations

Like all models, CoCoNet represents a highly simplified abstraction of the real system that excludes many components that are assumed to play a lesser role. For example, the role of water quality in supporting COTS larvae and subsequent outbreaks continues to be debated and has been removed from the model until some level of consensus emerges (Milne et al. 2023). Trophic pathways are still mostly unresolved or inferred from correlative studies. At the same time, COTS larvae are known to be consumed by damselfishes and other planktivorous fish (Cowan et al. 2017), but with predation rates unknown, their effect could only be represented as part of a broader COTS larval mortality term. Other predation rates are also uncertain, particularly in relation to cryptic benthic invertebrates. The representation of management interventions is also uncertain. For example, the emperor stock augmentation modelling scenario was purely theoretical, and while there is potential in restocking other species (e.g. snapper *Chrysophrys auratus* by the South Australian Research and Development Institute; herbivorous and planktivorous fishes) (Abelson et al. 2016; Obolski et al. 2016; Cortés-Useche et al. 2021), the production of emperor juveniles for annual release and their survival on real GBR reefs is untested. These are just examples of ways in which model result interpretations must be viewed with caution and will need to be supported by multiple lines of evidence before being used in decision-making.

The metrics used to measure the performance of intervention strategies are also highly simplified. Using the single metric of live hard coral cover summarised across the entire GBR provides a simplistic view of the desirable attributes of a “healthy” coral reef ecosystem. However, corals are the ecosystem engineers, and highly sensitive to climate change impacts as well as COTS predation. Coral cover is a globally accepted, robust metric to assess the severity of impacts to coral reefs and the pace of recovery (Emslie et al. 2024), and has a proven track record of sensitivity to COTS outbreaks at a GBR-wide scale (De'ath et al. 2012). COTS preference for fast-growing *Acropora* species, and the tendency for these corals to rapidly recolonise reefs in disturbance-free periods and dominate coral cover estimates (Vessaz et al. 2022), arguably enhances coral cover as a useful metric in this context. However, we acknowledge that coral cover alone does not equate to reef health, diversity, functioning or resilience (Streit et al. 2024), and that framing the results of our models in terms of coral cover gains should be viewed as a starting point from which to investigate multiple additional lines of evidence.

After utilising published and other available ecological data for parameterisation, the model was calibrated almost exclusively against LTMP data for coral cover, COTS outbreaks and fish densities. While LTMP survey methods provide relatively robust estimates of coral cover, they have much higher uncertainty in relation to COTS, which can be highly cryptic as juveniles and smaller adults. This limitation has been at least partially offset by focusing on outbreak rates (when numbers are high and individuals tend to be less cryptic) rather than abundances. LTMP surveys are also not ideal for adequately capturing emperor abundances (producing highly zero-inflated data). Attempts to correct LTMP emperor data using baited remote underwater video systems data have been limited by large disparities in the spatial scales of sampling (Cheal et al. 2021).

Fisheries catches were prescribed in the model based on aggregated commercial and charter data (derived from QLD DPI data). This approach neglected any under-reporting within these fisheries, as well as data from recreational fishing that has only been available from boat ramp surveys since 2015. The model also assumed negligible non-compliance with fisheries regulations, such as zoning. While compliance in GBR no-take zones is known to be far from perfect (Bergseth et al. 2015), there was no robust compliance data that could be incorporated into the model. All of these sources of under-reporting were represented by assuming that catches were 50% higher than reported. While plausible, this figure remains an important source of model uncertainty.

4.5 Where to next?

The CoCoNet model continues to be refined as new empirical data becomes available and process understanding improves. Research into identifying the predators of COTS and estimating their predation rates is ongoing, and our understanding of the complex food web and the ability for predators to control COTS is still in its infancy. Within the CCIP program, empirical evidence for predation by benthic rubble invertebrates (e.g. decorator crabs *Schizophrys aspera*: CCIP-P-05 Wolfe et al. 2025) and fishes (CCIP-P-06 Doll et al. 2025) is essential for integrating into models and to understand the level to which control of COTS by predators might be achieved. A new study found the density of the cryptic decorator crab was significantly related to the mean annual number of COTS culled (Wolfe et al. 2023); these species may benefit from zoning or fishery management interventions if an increase in predatory fishes lead to a reduction in invertivorous fish such as triggerfish and, therefore, an increase in invertebrates such as decorator crabs.

Future modelling studies will need to consider alternative climate scenarios, particularly the SSP2–4.5 (2.7ºC global warming) projection widely considered to be the most likely. In this context, biocontrol and other measures may need to temper expectations towards limiting coral decline, rather than fostering enhancement. A broader range of interventions and combinations of interventions will also need to be considered, exploiting the synergistic effects of fish protection measures, direct COTS control, and other coral protection and restoration strategies. For example, the existing scenario results suggest that benefits to corals delivered by historical rezoning could be further enhanced by a modest expansion of no-take zones (up to 40%). In the context of warming climate, new no-take zones could include recently identified climate refugia areas on the GBR (Sun et al. 2024). While the strategy combinations tested here did not significantly outperform individual strategies, many combinations remain to be identified and explored.

4.6 Conclusions

Despite the perceived future benefit of the COTS Control Program and sustained fisheries and spatial reef management on the GBR, coral reefs face multiple and increasing stressors in the Anthropocene (Ellis et al. 2019). All model scenarios assumed that future climate would follow the SSP1–2.6 (1.8ºC global warming) in terms of the frequency and severity of marine heatwaves (McWhorter et al. 2022). This option was chosen to ensure that any benefits associated with interventions were not completely overridden by the climate signal. However, it is now considered a relatively optimistic scenario, with the more severe SSP2–4.5 (2.7ºC global warming) a more likely pathway (Hausfather and Peters 2020). After 2040, all management scenarios, including those directly benefiting coral communities, are likely to buckle under the pressure of escalating climate change; all restoration and adaptation efforts can be quickly reversed by mounting climate-induced disturbances (Anthony et al. 2020; Condie et al. 2021). Ramping up more of what is currently being done to manage fishing, reduce COTS outbreaks and protect coral cover will not be sufficient to provide positive benefits to coral communities in the future. Fish predation alone will not be effective against continued COTS outbreaks and larger, more pervasive drivers of agents of coral mortality such as climate change. However, we show that the role of fish through trophic interactions will remain a vital component among synergistic interventions that together aim to minimise the loss of corals. Indeed, there is overwhelming global evidence that no-take zones and fisheries management remain critical in an effective toolbox of marine protection. The resulting benefits to target species, biodiversity and habitat quality provide ecosystems with a boost in their ability to resist and recover from the increasing disturbance regime facing coral reefs in the Anthropocene.

The final outputs of this project include:

- The expansion, parameterisation and validation of the CoCoNet model to test COTS predator biocontrol scenarios;
- Assessment of the efficacy of fish predator biocontrol scenarios; and
- A ranking of the most effective approaches to prevent outbreaks and benefit coral cover in the short and long-term under one climate scenario.

5. RESEARCH SYNERGIES AND NEXT STEPS

The CCIP was designed to encourage and support collaboration among the projects and cultivated this through a series of workshops and other opportunities. Many of the projects made use of the findings of others throughout the duration of the CCIP, enhancing the work and providing a forum for sharing ideas and solutions. This project, CCIP-R-10, benefited – and in turn supported other projects – through ten key synergies, both within CCIP and to external stakeholders and end-users.

1. **CCIP-P-05 – Benthic predation in rubble (Wolfe et al. 2025)**. Model parameterisation of predation by invertebrates on juvenile COTS were based on published information and modified based on new results from empirical studies from CCIP-P-05.

2. **CCIP-P-06 – Fish predation rates and zoning (Doll et al. 2025)**. Model parameterisation of fish predation on juvenile and adult COTS was based on published information, as well as new results from empirical studies. The relevant model parameters were reviewed by CCIP-P-06 lead, Morgan Pratchett.

3. **CCIP-R-08 – Stakeholder perceptions and co-benefits (Paxton et al. 2025)**. Consultation with the Reef Authority and QLD DPI were instrumental in designing scenarios.

4. **CCIP-R-09 – Reef Traditional Owner values assessment (Backhaus et al. 2025)**. Conversations with Vincent Backhaus were instrumental in developing communications products for Traditional Owners (TO).

5. **CCIP-R-03 – Reef-scale modelling (Rogers et al. 2025)**. Strong ties between our two projects, which used different models and tested scenarios under different circumstances, but both used a representation of fish predation and the relationship with fisheries.

6. **CCIP-R-05 – COTS dispersal ensemble modelling (Choukroun et al. 2025)**. Connectivity predictions used in CoCoNet were updated based on the results of this project, specifically around dispersal trajectories and connectivity matrices produced in collaboration with CCIP-R-05.

7. **The Reef Restoration and Adaptation Program (RRAP)**. The key publications on large-scale interventions at the inception of CCIP (e.g. Condie et al. 2021) were directly relevant to the formulation of CCIP-R-10.

8. **Queensland Department of Primary Industries (QLD DPI)**. Model parameterisation of fisheries pressures based on fisheries data from QLD DPI, under a Data Transfer Agreement with AIMS, and on human usage (e.g. recreational fisheries) data.

9. **AIMS Long-Term Monitoring Program (LTMP)**. Critical model input and validation data came from LTMP COTS, hard coral cover and coral reef fish surveys.

10. **Integrated Monitoring and Reporting (IMR) Reef Fish Monitoring Project**. There were synergies in TO engagement with IMR Integrated Reef Fish Monitoring Project (IM-CM-204-AIMS-Fish Phase1).

The following future research priorities are identified by this project:

- Research priority 1: Obtain better estimates of actual predation rates.
- Research priority 2: Explore the compliance element of zoning / fisheries management for inclusion into the model.
- Research priority 3: Explore a fishing pressure gradient vs COTS relationship rather than a zoning relationship.
- Research priority 4: Incorporate recreational fisher catch data and information from future stock assessments for emperors into models.
- Research priority 5: Explore predator biocontrol and COTS culling in the context of multiple future climate change scenarios.
- Research priority 6: Assess the implications of acute outbreaks versus chronically higher densities of COTS from a resilience-based management perspective (e.g. Nakamura et al. 2014).
- Research priority 7: Develop a better understanding of trophic relationships between fish and COTS, focusing on the indirect trophic pathways by which groupers might affect COTS outbreaks.

6. MANAGEMENT IMPLICATIONS AND IMPACT

To date, the protection of predatory fish has clear and proven benefits for coral reef ecosystems, including in the reduction of COTS and the resulting gains in coral cover. The results of our modelling study strengthen the understanding that boosting fish populations through zoning and fisheries management strategies has directly contributed to COTS control between 2004 and 2024. Hindcast modelling shows the positive effects of the actions taken in 2004 to enhance the protection of the GBRMP. Scenarios developed through this project focused on increasing these protection measures, especially zoning and fisheries management changes. Testing these scenarios with modelling offered a low-risk method of evaluating options that would be economically, socially and culturally difficult to implement in the real world. Our forecasting results suggest that further increasing zoning and fisheries restrictions are unlikely to be effective biocontrol measures that result in significant decreases in COTS outbreaks and increases in coral cover in the context of climate change. Protecting fish predators is a valuable tool in the resilience-based management context and complements other methods shown to effectively manage COTS outbreaks. All the abovementioned measures will eventually be overwhelmed by the impacts of climate change. This study adds to the understanding that an intact fish assemblage buffers reef health and resilience, and that on the GBR this is in part achieved through protecting the predators of COTS through zoning and fisheries management, which in turn sustains coral cover.

Governance, Engagement and Communications

Stakeholder engagement was undertaken strategically, considering the sensitivity of the project in relation to expectations around management scenarios. We opted for individual meetings rather than an all-in workshop, to ensure the most useful outcomes for end-users.

The scenarios to be tested by CoCoNet were designed in close collaboration with the Reef Authority as the main end user. There was a need to understand the effects of twenty years of ~30% no-take zone protection, and high priority was assigned to testing scenarios related to no-take zones and COTS Control Program effort, to ascertain potential benefits of future management strategies. Communications strategies were designed with the complexities of the project in mind, emphasising the theoretical nature of the project and the reliance of results on a series of simplifying assumptions about how reef ecosystem dynamics work, including fish predation rates on COTS.

COTS Strategic Management Framework

The scenarios feed into the Reef 2050 Plan by showing how much each scenario might contribute in terms of reducing COTS and enhancing coral cover. The model outputs show how changes in fish densities can influence COTS outbreaks, and to what extent this can contribute to the protection of reefs from outbreaks. By presenting the results in terms of quantitative coral gains, the scenarios help determine the benefits of deploying resources towards fish protection strategies.

Annual Reef Prioritisation Process

The confirmation that predator conservation strategies are currently providing benefits may have relevance for ongoing prioritisation of protected and unprotected reefs. However, a series of data streams and novel research are needed to confirm the robustness of our results in real ecosystems.

Final Remarks

Finally, CCIP-R-10 contributes to achieving the overarching outcomes and impacts identified in CCIP's Research Impact Plan by providing more accurate prediction of the effects of conserving COTS fish predators and identifying management scenarios that might benefit future coral cover on the GBR. While our aim was to simulate possible approaches to controlling COTS outbreaks in the next three decades, CoCoNet modelling with current knowledge corroborates the efficacy of current strategies (historical management Scenario 1) compared to no management (Scenario 0). An integrated approach is required to maximise the potential for future prevention of COTS outbreaks by 2050. Thus, combining conservation of COTS predators with current COTS management, interventions such as direct manual control, enforcement of no-take zones and fisheries regulations, may enhance efforts to support reef restoration and resilience in a warming climate.

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8. DATA ACCESSIBILITY

The model data generated in this study can be accessed at http://datadryad.org/share/xxGUGVuuflXrdIysXp3TJyM5BajOJYuKmItQt2AGYe8.

The model code developed within this study can be accessed at http://datadryad.org/share/xxGUGVuuflXrdIysXp3TJyM5BajOJYuKmItQt2AGYe8.

This excludes fisheries data provided by QLD DPI and restricted by a formal data agreement.

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APPENDIX A – SCENARIO DEVELOPMENT

The set of scenarios drafted for stakeholder consultation. This list was presented to the Reef Authority and QLD DPI, and the ensuing meetings and conversations served to focus and refine the list towards the final set of scenarios presented in this report.

N	Scenario	Zoning	Fisheries	Notes	Model implementation
1	No change	No change	No change	Counterfactual scenario	Apply historical catches 1986–2021
2	500 priority reefs for COTS control	No-take zones increase to 50%	Fishing displaced	Of the 500 COTS Control priority reefs, make sure 50% are green (if they aren't already)	Switch additional 647 reefs from blue to green - reefs selected randomly within each run of the ensemble
3	500 priority reefs for COTS control	No-take zones increase to 75%	Fishing displaced	Of the 500 COTS Control priority reefs, boost no-take zones to 75%	
4	500 priority reefs for COTS control	No-take zones increase to 100%	Fishing displaced	Turn all 500 COTS Control priority reefs to no-take	
5	500 priority reefs for COTS control	Change to no-take zone if identified as important COTS source reef (top x% of reefs)	Fishing displaced	x% needs to be determined based on model data	
6	500 priority reefs for COTS control	Change to restricted fishing (yellow) zone if identified as important COTS source reef (top x% of reefs)	Fishing displaced	x% needs to be determined based on model data	
7	500 priority reefs for COTS control	Change to no-take zone if identified as important coral source reef (top x% of reefs)	Fishing displaced	x% needs to be determined based on model data	
8	500 priority reefs for COTS control	Change to restricted fishing (yellow) zone if identified as important coral source reef (top x% of reefs)	Fishing displaced	x% needs to be determined based on model data	
9	Emperor correction factor	Regional correction factor for emperor abundance	No change		
10	Restocking emperors	No change	Aquaculture - no change in bag/size limits	Adding fish rather than removing them - to both no-take and fished zones	Apply historical catches 1986–2021, but add fish

N	Scenario	Zoning	Fisheries	Notes	Model implementation
11	Perfect compliance	No change	No change	If all existing fished zones had the fish stocks currently found in relevant preservation (no-entry, or pink) zones	Use fish density / biomass recorded from no-entry zones and apply it to no-take zones
12	No-take zones only	No-take zones increased to 100%	No fishing	Map extremes	Fishing removed
13	Fished zones only	No-take zones decreased to 0%	Fishing dispersed	Map extremes	All reefs open to fishing
14	No-take zones increased	No-take zones increase from 33% to 40%	Fishing displaced	Modest increase in no-take zones	Switch additional 266 reefs from blue to green - reefs selected randomly within each run of the ensemble
15	No-take zones increased	No-take zones increase from 33% to 50%	Fishing displaced	Large increase in no-take zones	Switch additional 647 reefs from blue to green - reefs selected randomly within each run of the ensemble
16	No-take zones reallocated	Change to no-take zone if identified as important COTS source reef (top x% of reefs)	Fishing displaced	x% needs to be determined based on model data.	Switch some blue reefs to green reefs - a reduction in fishing pressure at COTS source reefs
17	Restricted fishing (yellow) zones reallocated	Change to no-take zone if identified as important coral source reef (top x% of reefs)	Fishing displaced	Allows some fishing (one hook per line per person) would enable some fishing on a reef but less than a fished zone, thus reducing fishing pressure, more acceptable change	Switch some blue reefs to yellow reefs - a reduction in fishing pressure
18	Recreational bag limit	No change	Emperor recreational bag limit	Bag limit change to better protect confirmed COTS predators	Reduce recreational catches of emperors by 50%
19	Species-specific: vary size limit	No change	Increase minimum size limit	Size limits change to better protect confirmed COTS predators	Exclude emperor age classes from recreational catch (5+ years)
20	Species-specific: vary size limit	No change	Introduce maximum size limit	Size limits change to better protect confirmed COTS predators	Exclude emperor age classes from recreational catch (5+ years)

N	Scenario	Zoning	Fisheries	Notes	Model implementation
21	Commercial catch limit	No change	Emperor commercial catch limit	Catch limit change to better protect confirmed COTS predators	Reduce commercial catches of emperors by 50%
22	Spawning closures	No change	Spawning season closure	Closures beyond the no-take zones	Compare scenarios with catches applied before/after spawning each year
23	Family-specific take ban	No change	Ban take on 500 priority reefs	Allow maximum predation on COTS	
24	Family-specific take ban	No change	Ban take on coral/COTS source reefs / COTS sink reefs	Allow maximum predation on COTS	
25	Combined changes	e.g. Scenario 2	e.g. Scenario 21	Etc… combinations of the above zone and fishery changes, plus maybe some new ones	
26	Combined changes				
27	Combined changes				
28	Combined changes				

APPENDIX B – RESULTS FOR MANAGEMENT SCENARIOS A, D, G AND H

Additional management scenarios that failed to generate substantial responses relative to the underlying variability among model runs. Solid lines indicate median trends with the colours corresponding to the tested scenario and black to the historical baseline (Scenario 1). Grey lines represent individual runs from the model ensemble (from which medians were calculated).

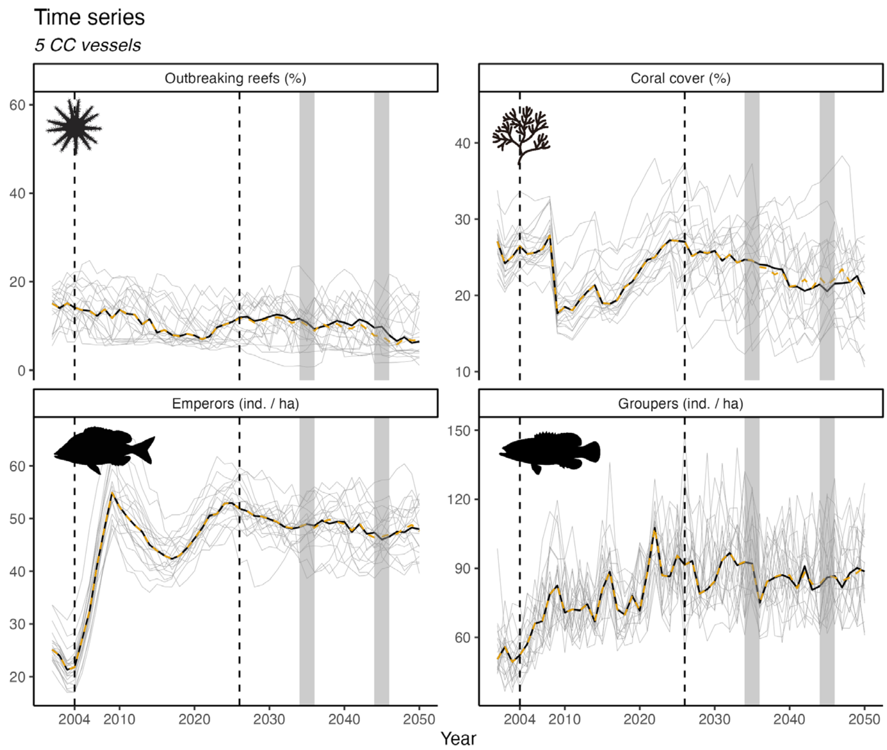

Figure B1. Forecast model trends through time among the four response variables for the 5 COTS control vessels scenario (Scenario A). Solid lines indicate median trends: coloured line is Scenario A, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario A.

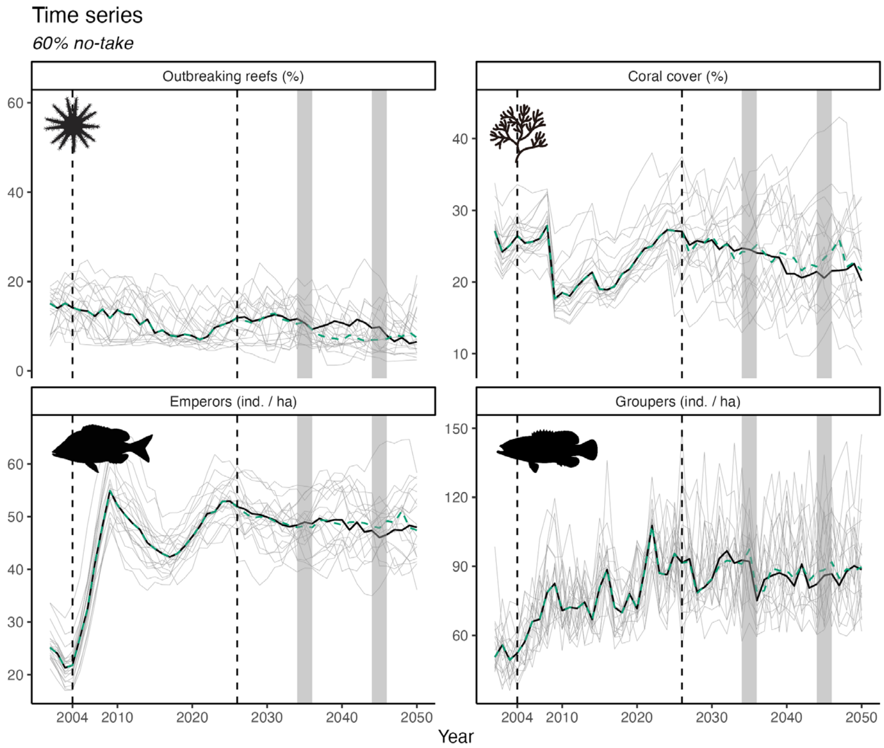

Figure B2. Forecast model trends through time among the four response variables for the 60% no-take scenario (Scenario D). Solid lines indicate median trends: coloured line is Scenario D, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario D.

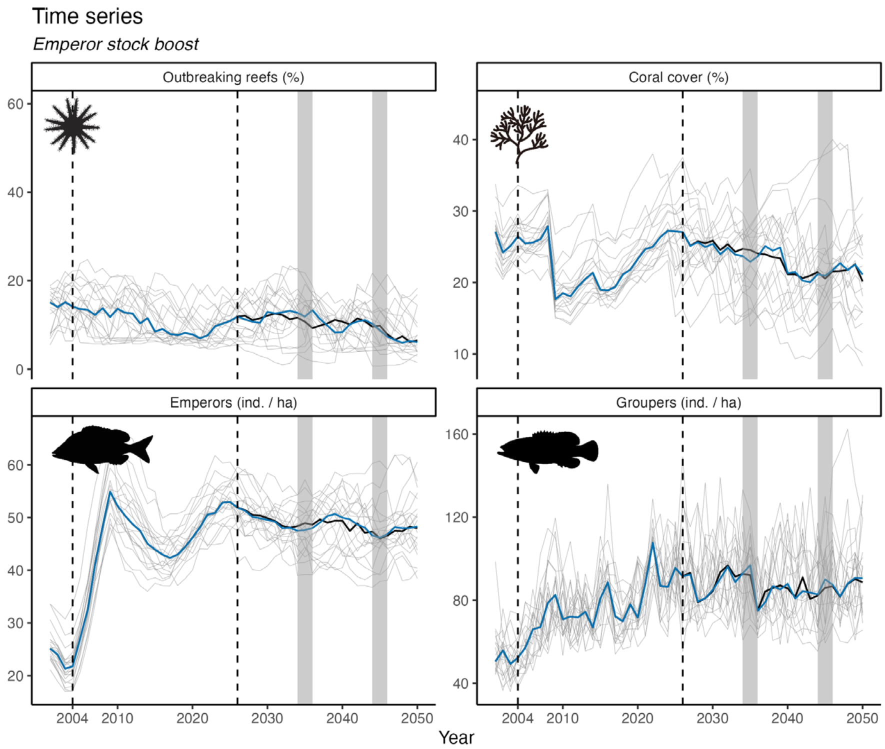

Figure B3. Forecast model trends through time among the four response variables for the emperor stock boost scenario (Scenario G). Solid lines indicate median trends: coloured line is Scenario G, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario G.

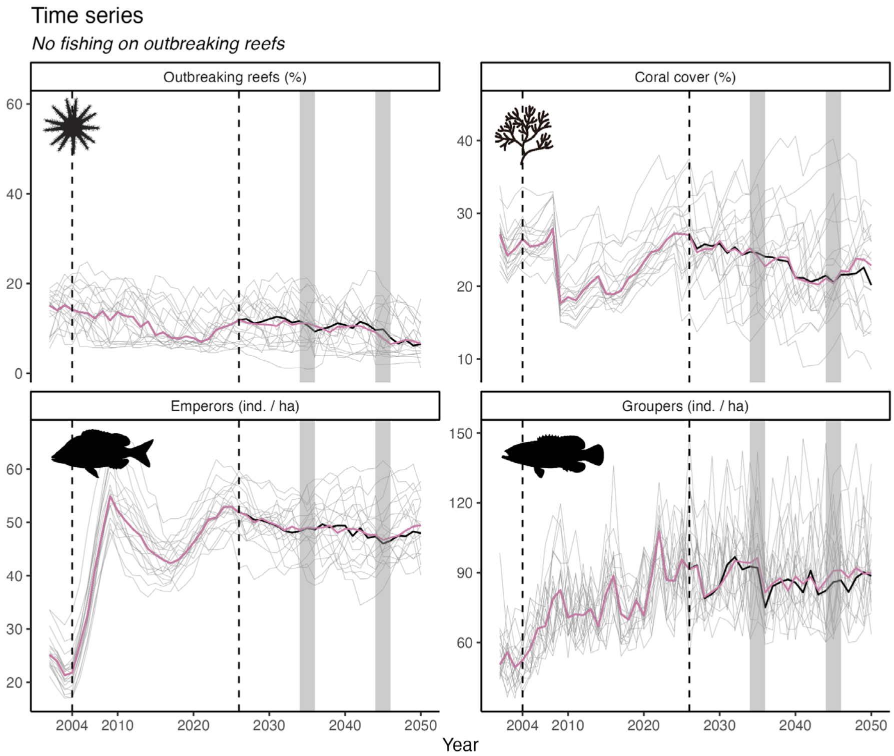

Figure B4. Forecast model trends through time among the four response variables for the no-fishing on outbreaking reefs scenario (Scenario H). Solid lines indicate median trends: coloured line is Scenario H, black line is the historical scenario (Scenario 1), and grey lines are individual runs from Scenario H.

APPENDIX C – COMPARISON OF COCONET AND LTMP

Examining how the average no-take-to-fished-zone ratios (2004–2022) compared between CoCoNet's Scenario 1 (Historical management) and LTMP monitoring data (254 reefs) by GBR region (e.g. northern, central, southern), there was 50% alignment across factors and regions (i.e. 9 of 12 plots show both sources above or below the line together) (**Figure C1**). It is likely that the difference between the numbers of reefs in the two datasets has affected the results, and they therefore need to be interpreted with caution. In all three regions, CoCoNet hindcasts predicted a higher proportion of reefs with COTS outbreaks (defined as 15 COTS per hectare) in no-take compared to fished zones than LTMP manta survey data, perhaps reflecting a higher proportion of protected reefs in areas of high outbreak frequency. However, there was agreement between CoCoNet and LTMP data that COTS outbreaks were more numerous in fished zones than no-take zones in the Southern GBR (i.e. values below 1). Coral cover was higher on average in no-take zones in the Southern GBR, in agreement with LTMP manta tow data which showed relatively less coral cover in no-take zones in the North and Central GBR. CoCoNet hindcasts revealed greater average emperor and grouper densities inside no-take zones compared to fished areas in most GBR regions except for groupers in the Northern GBR. CoCoNet estimates of no-take zone efficacy for fishes were similar to LTMP estimates for groupers in all three regions but were different for emperors in the Central GBR. However, the estimated no-take:fished ratios of fish densities did vary widely between CoCoNet and LTMP in some instances. For example, emperor density ratios of >10 were recorded by LTMP in the Southern GBR whereas CoCoNet placed the ratio much lower at ~1 (**Figure C1**).

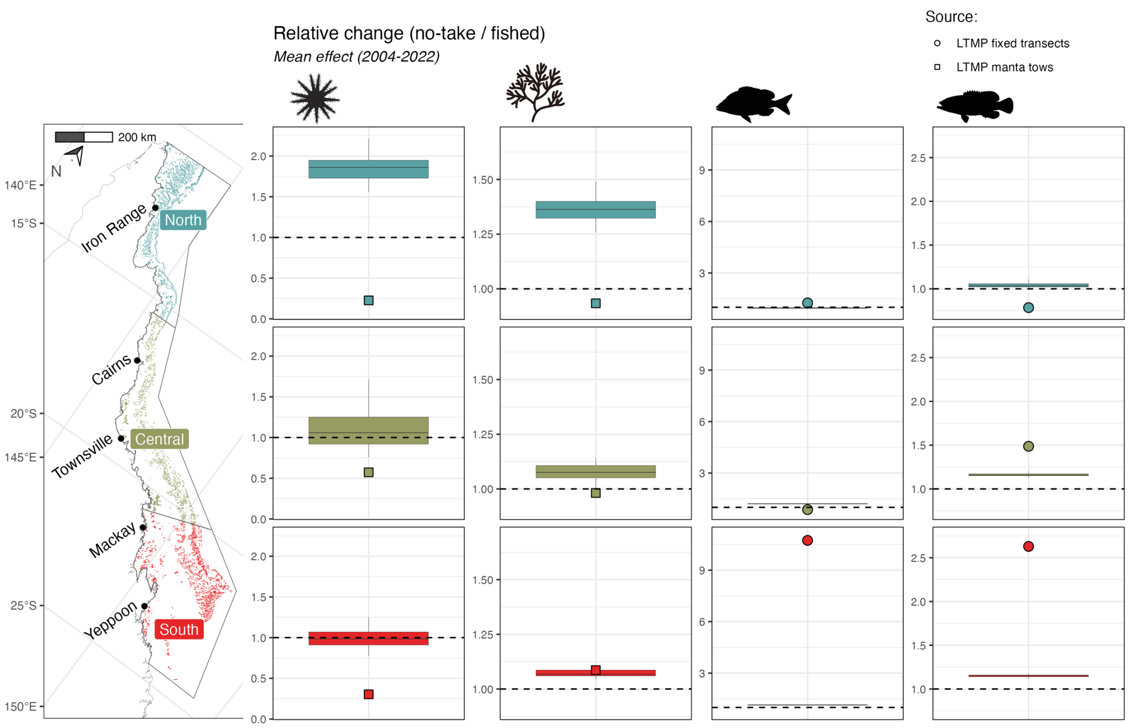

Figure C1. Model results comparing how the average no-take-to-fished (green-to-blue) -zone ratios (2004–2022) compare between CoCoNet's historical management scenario (rezoning to ~30% no-take, fisheries management regulations, Scenario 1) and LTMP monitoring data, partitioned by regions of the GBR (3,653 reefs). Each boxplot conveys the median ratio (central line), followed by the 25th and 75th percentiles (the lower and upper hinges). The upper/lower whiskers extend from each hinge to the largest/lowest value no further than 1.5 * IQR (inter-quartile range) from the hinge. Plot columns, from left to right, comprise the: proportion of COTS outbreaking reefs, coral cover, emperor density and grouper density. Dotted horizontal line indicates equal numbers of each variable in no-take zones and those open to fishing.

APPENDIX D – RESULTS FOR MANAGEMENT SCENARIOS K AND L

Additional management scenarios that either failed to generate substantial positive responses (size limits on catches) or combinations of scenarios that failed to perform better than scenarios deployed individually (no-take combined with COTS control).

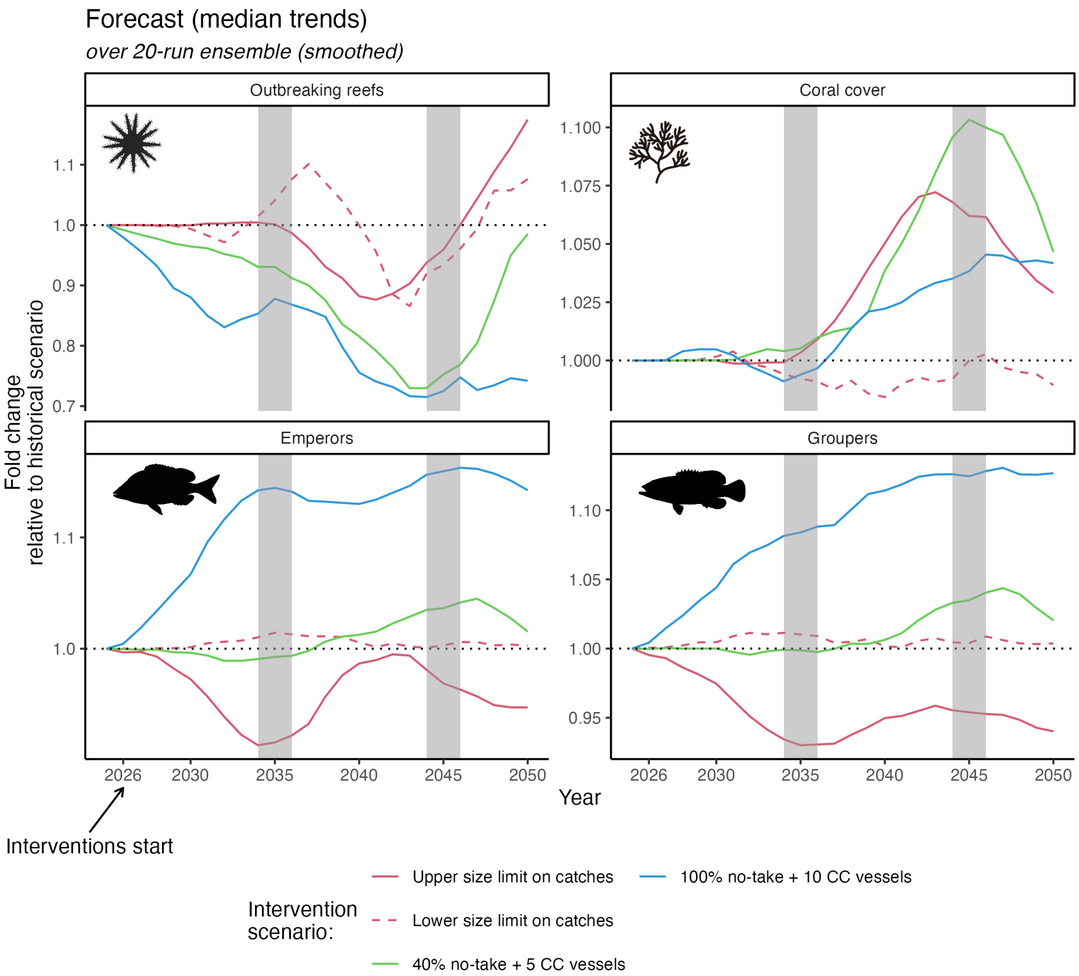

Figure D1. Model results comparing the fold change in median trends in hypothetical management scenarios (starting at 2026) to the historical management scenario (CC vessels refers to COTS Control Program vessels). Trends have been smoothed using a 6-yr moving average window. Y axes represent fold change (i.e. management scenario divided by historical management scenario) for proportion of reefs with outbreaks, percentage coral cover, and number of fish (emperors and groupers) per ha^{-1}.

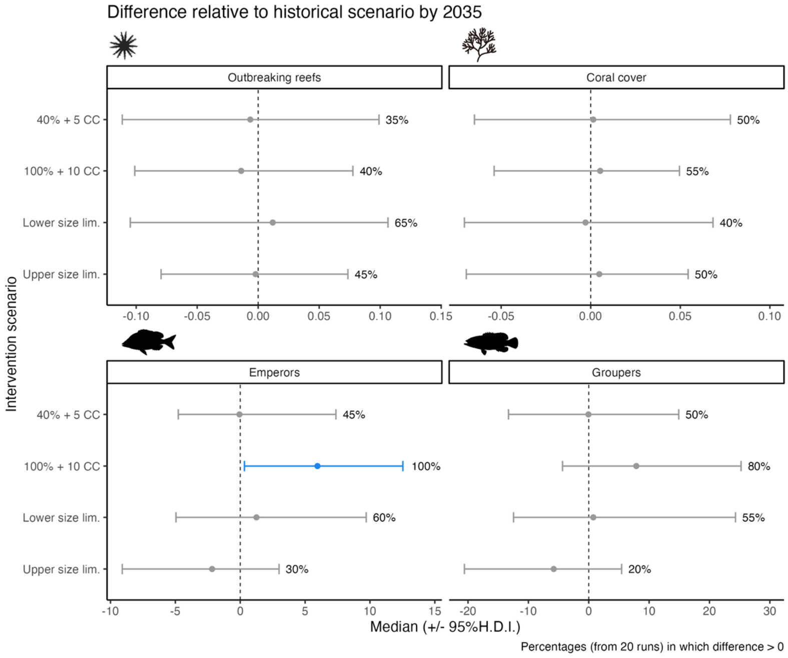

Figure D2. Differences between each scenario and the historical management scenario (Scenario 1) at the ensemble level in 2035. The median (circle) and the 95% H.D.I. across ensemble-level differences are presented, as well as the percentage of runs in which the difference was above 0. Red colour signifies 95% H.D.I. fully below 0, blue is fully above 0.

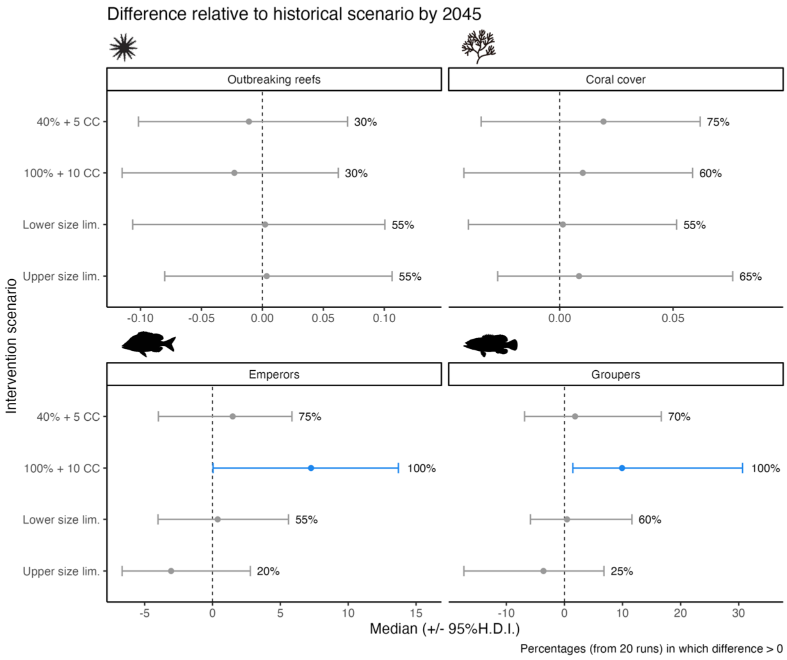

Figure D3. Differences between each scenario and the historical management scenario (Scenario 1) at the ensemble level in 2045. The median (circle) and the 95% H.D.I. across ensemble-level differences are presented, as well as the percentage of runs in which the difference was above 0. Red colour signifies 95% H.D.I. fully below 0, blue is fully above 0.

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