COTS Control Innovation Program

TECHNICAL REPORT

Dynamic models to inform crown-of-thorns starfish (COTS) intervention strategies at the reef-scale

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Dynamic models to inform crown-of-thorns starfish (COTS) intervention strategies at the reef-scale

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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

ADMB	Automatic Differentiation Model Builder
AIC	Akaike Information Criterion
AIMS	Australian Institute of Marine Science
BACI	Before-After Control-Impact
BOM	Bureau of Meteorology
CCIP	Crown-of-thorns starfish Control Innovation Program
COTS	Crown-of-thorns starfish
CPUE	Catch-per-unit-effort
CSIRO	Commonwealth Scientific and Industrial Research Organisation
eDNA	Environmental DNA
GBR	Great Barrier Reef
GBRF	Great Barrier Reef Foundation
GBRMPA	Great Barrier Reef Marine Park Authority
IPM	Integrated Pest Management
JCU	James Cook University
LTMP	Long-Term Monitoring Program
MICE	Models of Intermediate Complexity for Ecosystem assessment
MLE	Maximum Likelihood Estimation
MSE	Management Strategy Evaluation
QDAF	Queensland Department of Agriculture and Fisheries
RRAP	Reef Restoration and Adaptation Program
RHIS	Reef Health Impact Surveys
SALAD	Scooter-Assisted Large Area Diver-based
SCUBA	Self-contained underwater breathing apparatus
SST	Sea surface temperature
UQ	The University of Queensland

EXECUTIVE SUMMARY

The Pacific crown-of-thorns starfish (COTS, *Acanthaster cf. solaris*) is one of the leading causes of coral loss on the Great Barrier Reef (GBR). COTS are a voracious coral predator that undergo large population increases (irruptions), termed outbreaks. Controlling the density of COTS using manual culling methods is one way to help reduce the amount of coral that may be lost and provide opportunity for reefs to recover. In the past, culling focused on trying to eradicate COTS from economically important reefs after outbreaks were already underway. However, current management of COTS on the GBR uses aspects of Integrated Pest Management (IPM) to anticipate and strategically manage COTS populations by keeping COTS densities below where they cause net coral cover loss (“ecological management threshold”) or reducing densities to this point if they are found to be above it. The metric used to track COTS densities is the number of COTS culled within a given amount of dive time (called ‘catch-per-unit-effort’ or more simply, CPUE). Direct manual control requires many divers across multiple vessels and reefs and is an intensive and time-consuming process. Given time and resource limitations, it is important to direct COTS control capabilities most effectively to get the best possible outcomes.

Modelling to support management

Given the extent of the GBR, the use of models can provide valuable information about how to target and prioritise limited resources to get the best outcomes for the Reef. Modelling tools can help to identify and describe coral-COTS interactions and the processes linked to COTS outbreaks, providing valuable insight for management decision-making and supporting efficient and effective resource allocation. A number of different complementary models are available to support COTS management on the GBR. These models are mostly strategic in that they focus on whole of GBR processes and don’t formally condition the model on COTS Control Program data. Whole-of-GBR models provide valuable insight into general patterns and broad behaviours of ecological systems, however they often lack the required precision for evaluating the outcomes of local management, and require complex assumptions about system variability and interactions that are difficult to check. Specific management recommendations may not be effective at fine scales where outcomes can depend on local conditions (e.g. the composition of corals and COTS).

Localised models can make use of higher resolution data (e.g. daily data from the COTS Control Program), they reflect the local context better (e.g. result of culling on a given COTS population and how long it takes), and they can be more easily tailored to answer specific questions (e.g. performance of a culling threshold). Only versions of localised models provide the level of inference to robustly evaluate and test COTS management thresholds and control rules. This is because they allow for dynamic feedback between different population and management processes, and do not predetermine (or make assumptions about) their outcome. The local-scale COTS management model that has been used as part of COTS control is formally called a “Model of Intermediate Complexity for Ecosystem assessment” (or MICE for short).

Importance of ecological thresholds

The reason COTS are considered a pest species, despite their natural occurrence on the GBR, is because of their ability to rapidly consume corals at a rate faster than coral can recover. This requires understanding how COTS reduce coral cover and in turn, how the management action of culling reduces COTS density. The move to IPM introduced the

Simplified Decision Tree management strategy which uses the equilibrium coral-COTS threshold to ecologically align culling resources with coral growth rates and COTS predation. The aim is to try and balance COTS with the reef ecosystem to reduce coral loss given practical limitations of COTS culling. Getting all this right may provide opportunities for coral recovery and by only culling COTS down to the point where they are in balance with the reef ecosystem, the program maximises its potential impact from limited resources. Culling too low would use extra resources but with not much more impact.

The COTS Control Program currently uses a management culling target of 0.04 COTS.min^{-1} if coral cover is less than 40 %, and a COTS culling target of 0.08 COTS.min^{-1} otherwise. However, the point at which the balance of COTS and corals occurs may be different between reefs (e.g. due to different coral species and growth rates), and it is not known how differences in quantifying this ecological balance for management influences its effectiveness at avoiding coral loss. It is also important to understand how different management strategies compare in attaining this ecological balance. Complementary management options, such as enhancing COTS fish predator populations or using methods to influence starfish behaviours, also hold promise in maintaining ecological balance of coral and COTS on the GBR.

Advancing and validating a MICE for effective COTS control

In this project, we expand on, and further develop specially tailored versions of MICE, the sole local-scale COTS management model. The MICE simulates coral, COTS, and manual COTS control. We fit the MICE to daily data from 2018 to 2021 from the COTS Control Program (cull data and manta tow data) and Reef Health Impact Surveys (RHIS, for coral types at a location) so that it is formally validated and reflects observed trends in coral cover and COTS abundance. Having a validated model allows its use to reliably quantify the effectiveness of the current COTS Control Program. We also include reefs from different areas of the GBR so that the model can provide advice on a range of reefs that may have different conditions. Furthermore, we critically evaluate and inform the currently used management thresholds that underpin the COTS Control Program.

We recognise the ongoing work into management options for COTS other than culling, such as by enhancing or protecting COTS predator populations as well as by using predator cues to change COTS behaviours. A framework is therefore developed that brings in predator interactions and how they may influence COTS; the framework will not only be useful in the future for the MICE to simulate their effectiveness alongside manual control, but whole-of-GBR models may also adapt and build on the concept.

Integrated Pest Management created a transformative improvement in COTS control

As part of the adoption of the IPM approach, there was an important shift from culling all visible COTS at individual sites on a reef towards controlling COTS around the entire reef and only culling enough to avoid coral cover loss. IPM achieves this through a simplified decision tree. The simplified decision tree sets out the different choices and actions that determine whether COTS should be culled at a reef and how to do this in the most effective way. Models, especially the MICE developed in this project, are critical for providing guidance on the threshold values that are used in the decision tree. We simulated how the simplified decision tree, introduced in 2018 to inform COTS control strategies, might have protected coral cover compared to earlier management approaches (2013 to early 2018). We also assess the difference having a COTS control program makes by comparing model scenarios with and without control strategies (i.e. we simulate likely outcomes if there had not been any COTS control implemented).

The simplified decision tree was found to be far more cost and time effective than the historical approach that was used between 2013 and 2018. Specifically, we focused on four reefs near Cairns and found almost twice the amount of coral could have been saved. To think about this in an alternative way, to achieve comparable outcomes to historical control on these reefs would have required ~1,000 fewer dive hours which could have been invested elsewhere.

Examining recent data (2018–2021) for an expanded set of reefs and sites corroborated the favourable outcomes of the current COTS Control Program. Here we found that since 2018, across sites where COTS control work had been carried out, total coral cover was a median of about 7.2 % higher than if there had not been any control implemented. Our findings support that the amount of coral cover protected by the current COTS Control Program under IPM has substantially improved over historical approaches or no control scenarios. Notably there were two major bleaching events in 2016 and 2017 that we modelled, and simulating the simplified decision tree approach across these events highlighted that coral outcomes of the decision tree approach may be sensitive to such perturbations. The modelling suggested that reducing COTS densities was still beneficial. However, at sites where substantial bleaching has occurred, the MICE showed the thresholds guiding culling may be less effective and efforts could be more strategically deployed elsewhere. Even so, the IPM approach appears to promote resilience with the model suggesting that reefs affected by bleaching were likely to maintain higher coral cover and experience faster increases in coral cover compared to the historical approach or no control.

Effort Sinks

Building on previous work, we adapted the MICE to assess the performance of alternative COTS management scenarios using either the fertilisation threshold, or the equilibrium coral-COTS threshold delineated for management in different ways. These were considered under different voyage intervals where we used voyage intervals as proxy of the culling resources available. This work established a basis for dynamic control scenarios within the MICE (that we use and build on) and led to identifying a key management concept we termed “Effort Sinks”. Testing different scenarios revealed that, depending on the ecological threshold, certain reefs or sites could function as Effort Sinks—situations where COTS densities remain low but above the culling threshold, consuming substantial time and resources that could be more effectively allocated to other reefs or sites.

Advice on management thresholds to limit coral loss and facilitate conditions for recovery

With respect to revising current control thresholds, our modelling suggested that in general, current control thresholds remain fit for purpose. We found thresholds should be location specific if the objective of COTS control is coral recovery, but that location specific thresholds may not be needed if the objective is to limit coral cover loss (as opposed to recovering coral).

The consequence of overestimating the equilibrium coral-COTS thresholds in terms of coral cover loss is suggested to be limited at coral cover <40 % and varying control thresholds may make little difference. Between 40 % and 60 % coral cover, introducing an additional 0.06 COTS.min^{-1} threshold may help reduce coral loss. This study validates current COTS control on the GBR and suggests methods developed from localised studies can be more broadly applicable, and well-defined objectives (e.g. avoiding coral cover decline at a site) can help guide what thresholds are used and the sensitivity around these.

Advice on management thresholds to account for COTS population structure

If the management objective is to avoid coral loss due to COTS and facilitate conditions under which corals could recover, then based on our modelling analyses, the recommendation is to use the current control threshold irrespective of whether larger or smaller COTS make up the culled individuals. CPUE metrics do not convey information on the composition of small versus large COTS and this could impact how well the ecological management threshold captures the coral-COTS balance at a reef. We examined how the composition of a COTS population may vary between small and large individuals and recommend the current threshold is already conservative enough for populations with more or less smaller COTS, i.e. 0.04 COTS.min^{-1} for coral cover <40 % and 0.08 COTS.min^{-1} otherwise (or with an additional 0.06 COTS.min^{-1} tier for 40–60 % coral cover).

The current threshold does slightly overshoot the equilibrium balance between coral and COTS if the population has only small COTS that are hard to find. Deploying culling resources to reduce COTS populations below the current threshold levels for populations of small COTS is likely to have little benefit and be difficult to do given practical limitations. For example, CPUE can only be calculated post-dive (and therefore lags real-time), and COTS become increasingly harder to cull as densities decline (diminishing returns are more rapid if COTS are small). If a population is made up of larger COTS, then the current threshold is below where coral and COTS are in balance and, unlike smaller COTS, larger individuals are easier to locate, and densities should reduce faster to the management threshold. For the management objective of limiting coral loss and facilitating conditions under which corals could recover, then the current control thresholds remain fit for purpose.

Findings on management thresholds to limit COTS reproductive potential

In the future, if the management objective was to limit COTS reproductive success—which is not currently the stated objective—then a dynamic target, based on the catch of larger versus smaller COTS, is suggested. Based on our work here, a rule of thumb for attaining the fertilisation threshold would be culling no more than 6–7 COTS.ha^{-1} which includes no more than a density of 2 COTS.ha^{-1} of larger (>150 mm) COTS. This could be assessed using the cull data for a reef or site. Unlike using cull numbers or density, it is not recommended to specify CPUE targets for different COTS age classes as individuals are not culled independently of each other, which could lead to complex and unanticipated threshold behaviour. Instead, a flat CPUE may be preferred and then limiting COTS reproductive potential may be targeted through using the fertilisation threshold which is a CPUE of ~0.03 COTS.min^{-1}. Considering the potential limitations of CPUE, a low management target of 0.01 to 0.02 COTS.min^{-1} would be mostly consistent with reducing COTS populations to the point where they cannot reproduce as effectively. This would be a conservative target that accounts for COTS population composition. However, targeting very low thresholds such as <0.03 COTS.min^{-1}, or via the above rule of thumb, may lead to Effort Sinks and we therefore only recommend targeting the fertilisation threshold when an outbreak is not occurring or very early on during an outbreak when not many reefs are involved and thus resources can be extended at a few reefs (i.e. when trying to prevent or contain a new outbreak).

Conclusion

In summary, our research contributes quantitative analyses that can help to optimise choice of COTS control thresholds so that the available resources can achieve the greatest impact. The MICE approach is valuable in terms of integrating available data and understanding into an objective framework to support decision making. Additional questions and complexity were added to the coral-COTS MICE in a stepwise manner throughout this project to address emerging and high priority questions including climate change effects, predation impacts and how decisions are made. There is considerable scope to build on this framework into the future to continue to improve/refine COTS management on the GBR.

1. INTRODUCTION

Corals of the Great Barrier Reef (GBR) are exposed to a myriad of ongoing and escalating disturbances (e.g. De'ath et al. 2012; Ortiz et al. 2018; Condie et al. 2021) including losses due to the Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*; hereafter COTS). COTS are a naturally occurring coral predator, whose populations have periodically irrupted (commonly referred to as "outbreaks") on reefs across the GBR. At high densities, COTS populations can cause substantial coral loss (Pratchett et al. 2014). Whilst broad-scale stressors, including the impacts of ocean warming and acidification (which requires global action to mitigate effectively), are beyond the scope and capability of immediate on-water management methods and approaches, the impacts of COTS can be managed through local actions (Babcock et al. 2020; Westcott et al. 2020; Condie et al. 2021; Westcott et al. 2021b).

1.1 Integrated Pest Management for COTS

On the GBR, a COTS Control Program based on the principles of Integrated Pest Management (IPM) has been implemented. IPM for COTS combines aspects of their biology, life history, and interactions within their ecosystem to inform strategic culling to mitigate their damaging impacts on coral communities (GBRMPA 2020). COTS densities are manually controlled by divers who cull individuals using one-shot lethal injection (Bos et al. 2013; Rivera-Posada et al. 2014b). From 2013 to 2018, the approach to COTS control across the GBR was somewhat ad hoc, prioritising and visiting reefs mostly with high economic importance and culling starfish densities to as close to zero as possible (Westcott et al. 2020; Westcott et al. 2021b). From 2018, a more formalised culling operation was introduced based on IPM and Adaptive Management principles. The IPM approach uses a simplified decision tree to structure culling operation decisions in response to incoming surveillance and culling data, and to identify and track reefs for future control (Fletcher et al. 2020; Westcott et al. 2021 a, b). Under the IPM approach, the primary management objective is to prevent coral loss by reducing COTS densities to ecologically sustainable levels where the amount of coral they consume is less than or equal to the amount of coral that regenerates through growth (Fletcher et al. 2020; Plagányi et al. 2020).

Implementation of IPM depends on thresholds that define a permissible pest population based on whether the impacts from that population are deemed acceptable or not. On the GBR, management aims to identify and target reefs where COTS pose a risk to economic interests (e.g. reefs used for tourism) and/or an ecological risk (e.g. reefs that could support greater spread of outbreaks). It may not be possible to avoid all ecological and/or economic risks from COTS interacting with corals. In practice, COTS control aims to prevent (or at least reduce) the loss of coral cover due to COTS predation (Westcott et al. 2020; Westcott et al. 2021b). However, given time and resource limitations, it is not feasible to implement COTS control across all necessary reefs to mitigate outbreak impacts on the GBR. It is therefore important to ensure existing capability is used as effectively as possible to achieve meaningful management outcomes.

Modelling tools can be used to identify and describe coral-COTS interactions and processes associated with COTS outbreaks to inform management decision making and guide efficient and effective resource use. Models of Intermediate Complexity for Ecosystem Assessment (MICE) are well-suited to address targeted management questions and objectives, given they focus on a small set of species and ecosystem processes (Plagányi et al. 2014; Collie et al. 2016). MICE are built around, and formally fitted to, available data with the aim to provide robust advice, similar to fisheries models but with increased ecosystem context (Holsman et al. 2016; Plagányi et al. 2022). Importantly, MICE capture process outcomes rather than attempting to resolve unnecessary, and often uncertain, ecological complexity. For COTS and coral on the GBR, MICE provide a suitable framework to inform management thresholds underpinning COTS management and formally assess how different approaches to COTS control may influence coral cover trajectories.

1.2 Thresholds to support COTS management

Equilibrium coral-COTS thresholds (**Table 1**), defined as the point where COTS impacts on corals balance growth of the corals upon which COTS are feeding, can inform management targets aiming to prevent coral loss (Babcock et al. 2014; Plagányi et al. 2020). Equilibrium thresholds for the GBR have been established based on steady-state analysis of a MICE that relates the dynamics of two aggregated coral groups and COTS (Babcock et al. 2014; Morello et al. 2014; Plagányi et al. 2020; Rogers and Plagányi 2022). The model upon which the original thresholds were based (Morello et al. 2014) was fitted to Australian Institute of Marine Science (AIMS) Long-Term Monitoring Program (LTMP) data (% coral cover and COTS.manta tow^{-1}) from Lizard Island (northern mid-shelf GBR). Above the defined equilibrium threshold, the impacts of COTS exceed the capacity of corals to recover, and coral cover is expected to decline. Currently, equilibrium coral-COTS thresholds inform key COTS ecological management thresholds (**Table 1**) and are defined in terms of catch-per-unit-effort (CPUE, COTS culled per diver minute) to directly guide on-water culling activities (Babcock et al. 2014; Fletcher et al. 2020; GBRMPA 2020; Plagányi et al. 2020).

Table 1. Overview of current thresholds for COTS control on the GBR.

Equilibrium coral-COTS threshold	Point where coral growth is equal to coral loss arising from COTS population. It is expressed in terms of a COTS density (COTS.ha^{-1}). Theoretically there is no change in coral at the equilibrium threshold due to COTS. The threshold varies depending on coral abundance (Plagányi et al. 2020).
Fertilisation threshold	A density of COTS where reproduction becomes relatively harder. For the GBR this threshold is 3 COTS.ha^{-1}. Below this density, COTS reproductive success has been suggested by modelling to decrease sharply (Rogers et al. 2017).
Ecological management threshold	Management target for the removal of COTS from a management site. Target is based on the Equilibrium coral-COTS threshold (above) and practical considerations. The ecological management threshold is currently expressed in terms of Catch-Per-Unit-Effort (CPUE) and is specified as a target of 0.04 COTS.min^{-1} if coral cover is < 40 % or 0.08 if coral cover is ≥ 40 % (Babcock et al. 2014; Fletcher et al. 2020; GBRMPA 2020).

The current management thresholds are applied to all reefs of the GBR and it is not known if, or how, thresholds could be refined to improve COTS control efficiency. Two key processes that inform the underlying equilibrium coral-COTS thresholds are (1) the growth capacity of corals (Babcock et al. 2014; Plagányi et al. 2020), and (2) the effect of COTS detectability on CPUE. Equilibrium thresholds are therefore likely to be different depending on the coral assemblage, geographical location, recent thermal history, and COTS demography. Furthermore, in some locations managers may want to consider COTS reproduction suppression (Fertilisation threshold, **Table 1**) as the key objective to limit their potential spread between reefs, and this involves reducing COTS to even lower densities than those required to limit coral loss (Rogers et al. 2017; Plagányi et al. 2020). Within-reef management strategies could be refined and matched to different reefs based on reef conditions and reef-specific management objectives. However, the first step to achieve that is to understand how appropriate current COTS control thresholds are for different areas of the GBR and whether this might influence coral outcomes. It is also important to gauge how using different thresholds under resource constraints (e.g. voyage capacity) could impact coral cover outcomes.

Coral population growth rates show both latitudinal and cross-shelf variation on the GBR (Bozec et al. 2022) and COTS management thresholds are based on analyses from a single location of the GBR (Lizard Island; Morello et al. 2014). In comparison to other areas of the GBR, Lizard Island has favourable conditions for coral growth (e.g. colony level for preferred *Acropora* taxa: Anderson et al. 2017; population level: Bozec et al. 2022) so the growth rates used to derive current equilibrium thresholds may be too high for some locations (or low for others). It is therefore important to evaluate whether the current equilibrium thresholds can be generalised across the GBR or whether they need to be refined for different locations and environmental conditions. Bleaching events may also compromise the growth capacity of corals (Glynn 1993; Hoegh-Guldberg 1999; Hughes et al. 2003) and require adaptive management 'as needed' and specific consideration. Refining management thresholds with inferences from simulated coral bleaching and COTS outbreak disturbances can support managers to develop within-reef COTS management strategies.

Another factor that may impact the implementation COTS control thresholds (e.g. the "ecological management threshold") is COTS detectability. In fisheries, when using CPUE to approximate underlying density or abundance, inferences can be sensitive to age-size selectivity (Maunder et al. 2006). Current manual control techniques in the COTS Control Program are strongly selective and biased towards larger COTS (MacNeil et al. 2016) with smaller COTS (<150 mm diameter) having much lower detectability than larger individuals (> 150 mm diameter) (Plagányi et al. 2020). Where targeting a specific population, or in being selective for a fraction of a population, then CPUE rates may remain similar and not reflect a decreasing underlying population abundance (particularly in species that aggregate or have patchy distributions), and this is known as hyperstability (Maunder et al. 2006). Where hyperstability occurs, it is ideal to contextualise abundance inferences with additional information and ecological or population dynamics theory (Maunder et al. 2006). Demographic skews in the COTS population may impact the expected CPUE and thus catch rates may not reflect population density. Strong skews of catches towards larger mature individuals may mean CPUE metrics potentially underestimate the reproductively relevant population density. Alternatively, demographic skews in the catch towards immature COTS may decrease the expected CPUE and thus catch rates may underestimate overall population density. The demographic composition of controlled (or surveyed/monitored) COTS populations is important and consideration of demographic uncertainty could improve the generality of CPUE thresholds on-water (i.e. interpreting CPUE with other complementary information and theory).

1.3 Model development to enable assessment of new COTS management strategies

Whilst recent advances, namely the development of single shot injections and the implementation of IPM principles, have greatly improved the effectiveness of COTS control (Westcott et al. 2021b; Matthews et al. 2024), further improvements may be achieved by combining direct manual culling with new COTS management strategies (Condie et al. 2018; Condie et al. 2021). These new strategies are the subject of ongoing work and include potential bio-chemical modification of COTS behaviour (Hall et al. 2017; Motti et al. 2022), and the management of COTS predators (Kroon et al. 2021). As these new strategies mature, modelling can be used to guide their deployment. However, in order to do this the modelling framework needs to be expanded to capture and link how COTS may interact with potential predators. To date, COTS models have only considered predators to remove individuals from the population and have not captured how the presence of predators may alter COTS cryptic behaviour (a basis for aspects of the COTS Control Innovation Program's (CCIP) research into bio-chemical modification of COTS behaviour; Motti et al. 2022).

Recently, the role of predators in COTS population dynamics has gained more attention with increasing numbers of species identified that likely consume COTS (Cowan et al. 2017; Kroon et al. 2020). Some of the species found to potentially consume COTS are fisheries target species (Kroon et al. 2020) and may play a role in COTS outbreak dynamics (Kroon et al. 2021). Areas where fish were caught had higher numbers of detected COTS (Kroon et al. 2021) than areas closed to fishing suggesting fish may play an important role in regulating COTS abundance. In addition to impacts on the density of COTS due to consumption by fish predators, predators may also influence the behaviour of COTS. For example, the presence of predators may restrict certain size classes (those at risk of predation) to refuges within the coral matrix, making them harder to detect, similar to what has been found for urchins (Smith and Tinker 2022). Moreover, in the presence of predators COTS may be more inclined to remain cryptic and hence reduce their feeding rates (upon which key ecological thresholds are partly based) and movement capacity. Behavioural modification similarly underpins research into COTS control strategies that aim to use semiochemicals to influence COTS movements between reef areas (Motti et al. 2022). Developing the MICE to examine predator and behavioural interactions alongside COTS movements is important for future simulation testing of synergistic within-reef management controls. These are of consequence in the deployment of control resources which rely upon estimates of COTS abundance and detectability and may support the development of new COTS management strategies. Changes to cryptic behaviour could modulate natural predators and culling efficiency. This project involved developing a framework compatible with common population dynamics models (e.g. MICE and CoCoNet) such that predator-linked COTS behaviour can be considered.

1.4 Project aims and pathway to impact

This project (CCIP-R-03) falls within the Response subprogram of the CCIP. It models coral-COTS dynamics at the reef scale with the overarching aim of refining COTS control thresholds and evaluating COTS control performance. This project thus contributes to the development of targeted decision support tools, allowing for a more efficient and effective operational response as shown by the pathway to impact in **Figure 1**. The overarching aim is distilled into the following specific, targetable, project aims that we hereafter address. These are to:

- Develop MICE to include the current management strategy for COTS control relevant for reef-scale modelling, identify reefs with sufficient recent data and fit the MICE to them, develop a framework for the MICE to account for fish as predators for future modelling of alternative management strategies.
- Refine equilibrium coral-COTS thresholds and ecological management thresholds (**Table 1** by assessing their sensitivity to variation in coral growth rates and the demographic composition of COTS populations.
- Evaluate the relative performance of different intervention strategies for management control of COTS populations at the scale of management sites and characterise efficacy of recent IPM-based COTS control.
- Evaluate the performance of the recent IPM approach (2018–2021) relative to the 'historical' approach (2013–2018) and relative to no control.

Publications and planned publications that have resulted from these aims, and that have directly and indirectly benefitted from CCIP, are summarised in **Table 8**.

Key synergies with other projects include (1) data provision from the Prediction subprogram (e.g. CCIP-P-01 In-situ feeding rates (Pratchett et al. 2025a), CCIP-P-05 Benthic predation in rubble (Wolfe et al. 2025), CCIP-P-06 Fish predation rates and zoning (Doll et al. 2025)) that could be used in future iterations of the model; and (2) linking with other decision support tools from the Response subprogram in any future work (e.g. CCIP-R-01 Information infrastructure (Fletcher and Rezvani 2025) and CCIP-R-04 Regional modelling (Skinner et al. 2025).

To prevent coral loss from COTS outbreaks, project aimed to improve the ecological underpinning and prioritisation of COTS management. This was achieved through leveraging an existing coral-COTS MICE to address known limitations of the current Control Program and exploring sensitivities of the thresholds that inform on-water control. Improvements to threshold estimates and understanding how generalisable existing thresholds are across the GBR has the potential to dramatically improve reef-specific responsiveness and efficiency of current control actions in limiting COTS-induced impacts and outbreaks. Thresholds must be subsequently operationalised in an efficacious manner. This requires resolving key ecological considerations alongside those of potential future management interventions. This project supported these aims by developing a framework for the MICE that can be used in the future to capture how predators and coral abundance and/or composition may influence COTS dynamics.

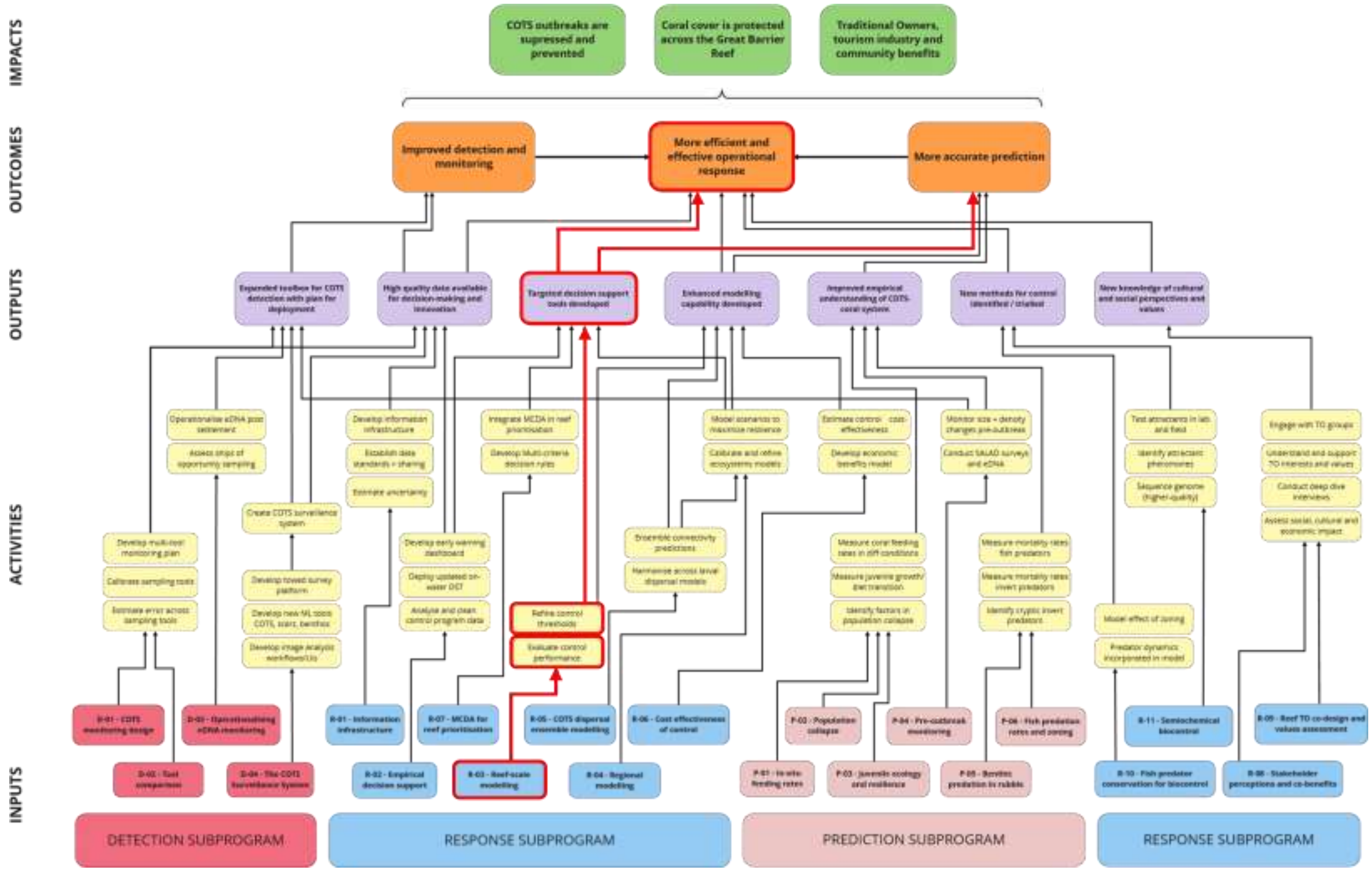


Figure 1. CCIP Program Logic showing project R-03 within the Response Subprogram and pathways to impact.

2. METHODS

2.1 Overview of modelling approach

Ecological modelling is a key approach to understanding and managing ecological systems (Plagányi et al. 2014b; Collie et al. 2016). There are many different types of models, from those that consider few ecosystem components and processes, through to those that consider many. The complexity of employed models has repercussions for the nature of the management advice they can provide—highly targeted, narrowly focused models are often capable of providing specific and tactical advice on key system components whereas broader models are able to offer more strategic insights and contextualisation (Collie et al. 2016). Models of Intermediate Complexity for Ecosystem assessment (MICE) focus on a small set of species and ecosystem processes needed to inform specific questions and objectives (Plagányi et al. 2014; Collie et al. 2016). MICE are built around, and formally fitted to, what data are available to inform them, and they aim to provide robust advice similar to fisheries models but with increased ecosystem context (Holsman et al. 2016; Plagányi et al. 2022).

2.2 Coral-COTS MICE

The coral-COTS MICE relate the dynamics of two aggregated coral groups and COTS (Babcock et al. 2014; Morello et al. 2014; Plagányi et al. 2020; Rogers and Pláganyi 2022; Rogers et al. 2023) (**Error! Reference source not found.**). The two modelled coral groups differ in their preferential predation by COTS and their growth rates. The first group includes fast-growing corals, representing species from genera such as *Acropora*, *Pocillopora* and *Montipora* which are preferred and targeted by COTS when available (Pratchett 2007). The second group includes slow-growing corals characterised by massive morphologies, such as *Porites* spp., which are consumed less than expected (Pratchett 2007) and considered non-preferred COTS prey (Morello et al. 2014). The MICE developed and applied in the CCIP project was substantially expanded from earlier reef-scale MICE and **Figure 3** shows a timeline of MICE development and application. **Table 2** and below we summarise key differences between the various coral-COTS MICE versions (for a detailed comparison with previous MICE versions, see Rogers (2022)).

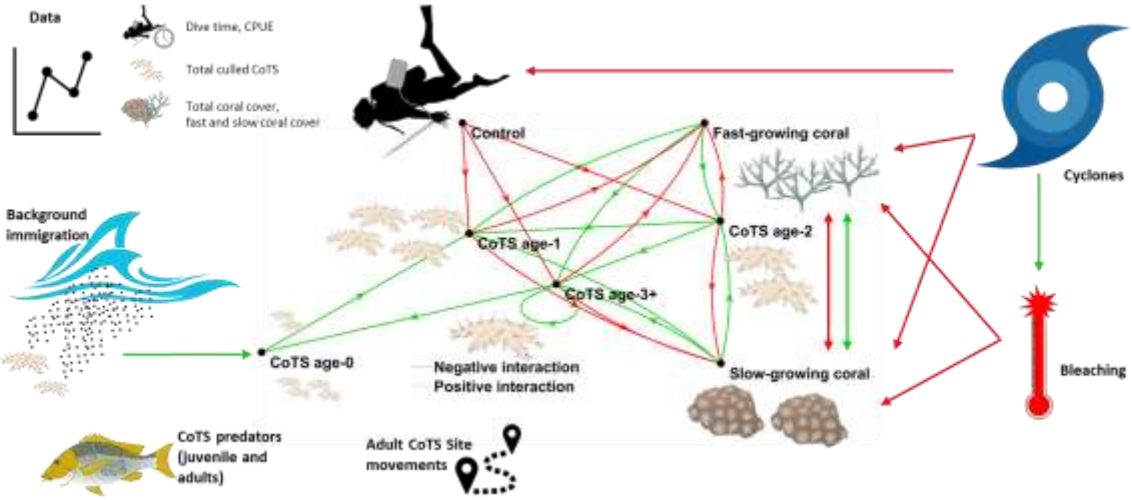
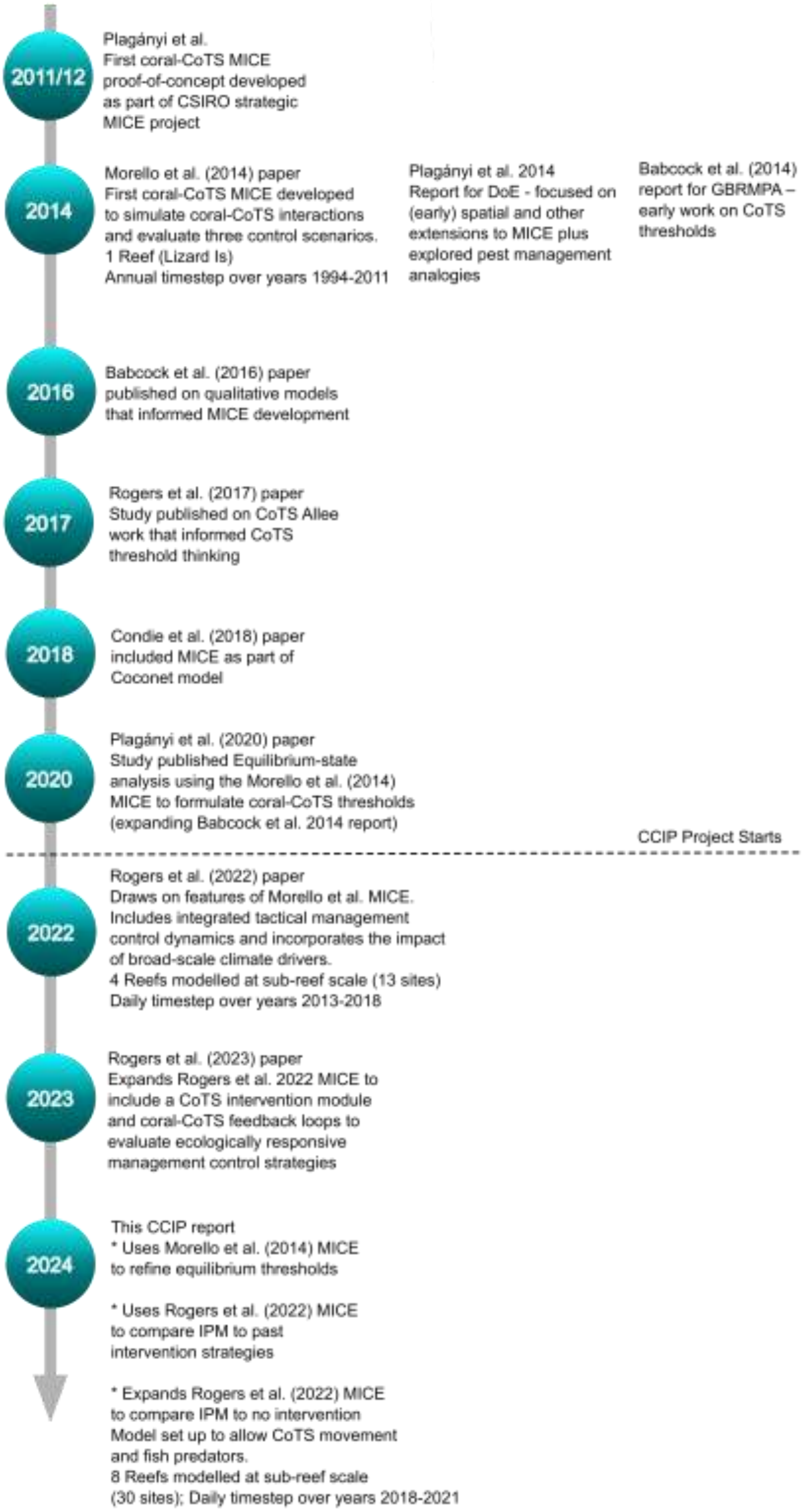


Figure 2. Schematic of coral-COTS MICE.

An important component of this CCIP project was to build on earlier work using an equilibrium state analysis to formulate coral-COTS thresholds The MICE version that is used for this purpose is that of Morello et al. (2014). The model complexity of the Morello et al. (2014) is simpler than subsequent model versions that have been built upon it as new questions were asked of it and more data became available (complexity is considered here in terms of how many components there are as well as how resolved they are). The structure of this MICE version means that it is tractable to assess its dynamics, and greater complexity is built into it to convert COTS densities into the CPUE rates that are relevant for managers and implementation (as per methods outlined in Plagányi et al (2020)). Specifically, the MICE is numerically solved to obtain approximations of the point at which COTS-coral interactions and associated impacts from COTS on coral balances coral growth and how COTS demography may impact these. The generality of currently implemented thresholds across different coral growth rates and COTS demographics has not been considered before.

Another component of the present work was to use the previously developed MICE version of Rogers and Plagányi (2022) (**Figure 3**) to compare how modern COTS management performs relative to historical COTS management, including how the 2016–2017 bleaching events may have impacted it. This required work to codify to the management strategy currently in use, and then integrate that into the feedback loops within the model. The Rogers and Plagányi (2022) model is at the sub-reef scale using data from four reefs (13 management sites) and a daily timestep. The model is fitted to data from the COTS Control Program for the years 2013–2018 and time series for model fitting were only suitable (number of control visits, regularity of control) for four reefs during the Programs' infancy. The model used the same two aggregated coral groups (i.e. fast- and slow-growing), but with coupled coral dynamics through a joint carrying capacity so that corals compete for space. Along with COTS predation, cyclone and coral bleaching mortality terms were also included. COTS were modelled using an expanded age-structured model compared to Morello et al. (2014), with four age classes built around the reporting structure of the culling data instead of three age classes. A background immigration recruitment rate was also estimated for each site and a stock-recruitment relationship that integrated key biological details was included. COTS removals were modelled as a function of age-dependent detectability, population structure, population density, non-linear relationship between COTS density and catch rate, and effort expended at a site. Together these inform the number of COTS removed from given age classes (see summary in **Table 2**).

In this project, we use different MICE versions to address different questions. This is because the different versions have different levels of complexity that are more suited to answering different questions. We use the Morello et al. (2014) MICE in a similar way to Plagányi et al. (2020) to revise ecological thresholds and consider demographic uncertainty (see section 2.5). We use the Rogers and Plagányi (2022) MICE to assess how well IPM would have performed compared to the ad hoc control approach that was used over the period 2013–2018 (see section 2.6). We then build on the Rogers and Plagányi (2022) MICE by fitting it to data from the current Control Program using more recent data (mid-2018 to mid-2021). The need to update the model to accommodate post-2018 data was because there were changes in operation of the Control Program (e.g. standardising site size) which broke the time series in site-dependent information (e.g. coral cover) and there were new data made available. These new data include manta tow and Reef Health Impact Survey (RHIS) data which are used to inform coral dynamics in the model, and culling and effort data from the COTS Control Program which informs COTS dynamics. The new data covered more reefs across different sectors of the GBR, increasing spatial coverage from four reefs (13 management sites) to eight reefs (30 management sites) (see section 2.4). We use this model to compare efficacy of the IPM approach to no intervention (see section 2.6) and develop a framework for including fish predator impacts on COTS in the future (see section 2.7). This expanded MICE and framework now provides a tool for testing alternate control strategies in the future.



2011/12
Plagányi et al.
First coral-CoTS MICE proof-of-concept developed as part of CSIRO strategic MICE project

2014
Morello et al. (2014) paper
First coral-CoTS MICE developed to simulate coral-CoTS interactions and evaluate three control scenarios.
1 Reef (Lizard Is)
Annual timestep over years 1994-2011

Plagányi et al. 2014
Report for DoE - focused on (early) spatial and other extensions to MICE plus explored pest management analogies

Babcock et al. (2014) report for GBRMPA – early work on CoTS thresholds

2016
Babcock et al. (2016) paper published on qualitative models that informed MICE development

2017
Rogers et al. (2017) paper
Study published on CoTS Allee work that informed CoTS threshold thinking

2018
Condie et al. (2018) paper included MICE as part of Coconet model

2020
Plagányi et al. (2020) paper
Study published Equilibrium-state analysis using the Morello et al. (2014) MICE to formulate coral-CoTS thresholds (expanding Babcock et al. 2014 report)

CCIP Project Starts

2022
Rogers et al. (2022) paper
Draws on features of Morello et al. MICE.
Includes integrated tactical management control dynamics and incorporates the impact of broad-scale climate drivers.
4 Reefs modelled at sub-reef scale (13 sites)
Daily timestep over years 2013-2018

2023
Rogers et al. (2023) paper
Expands Rogers et al. 2022 MICE to include a CoTS intervention module and coral-CoTS feedback loops to evaluate ecologically responsive management control strategies

2024
This CCIP report
* Uses Morello et al. (2014) MICE to refine equilibrium thresholds

* Uses Rogers et al. (2022) MICE to compare IPM to past intervention strategies

* Expands Rogers et al. (2022) MICE to compare IPM to no intervention
Model set up to allow CoTS movement and fish predators.
8 Reefs modelled at sub-reef scale (30 sites); Daily timestep over years 2018-2021

Figure 3. Timeline showing coral-COTS MICE progress over the past 14 years.

Table 2. Summary of key features of the MICE developed and used in the CCIP project for modelling coral and crown-of-thorns starfish (COTS) dynamics. The component or dynamic header is highlighted in bold. Table adapted from Rogers (2022).

CCIP MICE	Rationale and justification
Data • COTS Control Program cull site total coral cover data, RHIS coral cover data, COTS catch-per-unit-effort data, COTS catches, dive time at site.	Data from the COTS Control Program for years 2018–2021 became available. The data from the Control Program was based on SCUBA instead of manta tows. Manta tow data detects few smaller (age-1) COTS where COTS have higher cryptic rates. SCUBA-based approaches (e.g. COTS Control Program) are able to locate cryptic individuals in the reef matrix over repeated visits.
Time and spatial scale • Sub-reef spatial scale (8 reefs/30 management sites). • Daily time scale.	Data from the COTS Control Program was available at the spatial resolution of COTS management sites. This allowed for the MICE to be developed at this scale. The sub-reef scale is the scale at which management decisions are often made (e.g. which sites at a reef to control) which allows the model to provide information on how to use management thresholds and identify factors that may limit the effectiveness of control at a site (e.g. bleaching). A daily time step allows ‘decisions’ about which site to control to be made each day of a voyage similar to how control decisions are made on-water (which are in turn based on how control progresses at sites).
COTS population age-structure • Age-structured. • Four age classes (0,1,2,3+).	The COTS Control Program interacts differently with COTS depending on their age/size. The smallest COTS (age-0) escape the Program, age-1 have low detection and catch rates (a detectability of 19 %), and age-2 and age-3+ have relatively high detectability (a detectability of 82 %). Differences in COTS detectability, and therefore how easily they can be removed, can have an impact on population structure and result in fewer larger COTS (Westcott et al. 2020). The largest COTS (age-3+) can contribute the most to the reproductive output from a location (Babcock et al. 2016; Rogers et al. 2017; Pratchett et al. 2021). Capturing the persistence of the largest COTS (which is strongly influenced by COTS control) is an important consideration for local management and having a greater number of larger COTS could potentially prolong locally high COTS densities by increasing reproductive success (e.g. self-recruitment to a reef). Expansion of the number of age-classes was necessary for the relationship between the COTS Control Program and local recruitment factors to be included in the model.
COTS recruitment • Background immigration recruitment rate estimated for each site. • Included a stock-recruitment relationship that integrated key biological details (e.g. gonad weight, fecundity).	Settling COTS can recruit to a site either by being recruited from individuals within the site (self-recruitment) or by immigration from other areas on the same reef or other reefs. There are no data on the relative importance of these different sources but it is likely that each is more important at different times (e.g. as suggested by Morello et al. (2014)). Greater detail on COTS recruitment was included for two reasons, (1) to include the potential for both recruitment

CCIP MICE	Rationale and justification
• Recruitment variability estimated at reef level for years 2018–2021. Applied to sum of self-recruitment and immigration recruitment sources.	sources (immigration and self-recruitment), and (2) to allow for management activities to influence COTS recruitment dynamics. As no data is available for point 1, instead of attributing recruitment increases/decreases to immigration or self-recruitment, the sum of the two is scaled. Scaling the sum means recruitment fluctuations could be due to either, or some combination of, immigration and self-recruitment sources. For point 2, COTS culling disproportionately removes the individuals with the most reproductive potential (i.e. the largest COTS). Reproductive potential is inferred from gonad weight which exponentially increases with COTS size (Babcock et al. 2016; Pratchett et al. 2021). Female COTS are more important than males to population-level reproductive success within an area (Rogers et al. 2017). To capture how culling influenced reproductive potential, a novel variant of the Beverton-Holt stock-recruitment relationship was formulated in terms of female COTS and their potential contribution to self-recruitment. The culmination of these factors allowed for COTS populations to potentially persist at reefs beyond the collapse of immigration driven population increases (i.e. sustained by self-recruitment). This allows the model to infer the impact of COTS culling on local COTS persistence beyond only the removal of individuals. Capturing the impact of COTS control on population dynamics is an important element for cross-scale dynamics (e.g. recruitment between reefs (Condie et al. 2018)).
Coral population dynamics • Two aggregated coral groups (fast- and slow-growing). • Schaefer model with coupled coral dynamics through a joint carrying capacity so that corals compete for space. • COTS predation, cyclone, and coral bleaching mortality terms included. • Cyclones modelled stochastically. • Cyclone size, intensity/contours, and inflicted damage. • Adaptive/acclimation to bleaching events included. • Cyclones interact with bleaching events (could reduce severity – cooling) and if control could be conducted.	Corals compete for space. On the GBR COTS disproportionately target fast-growing coral (Pratchett 2007) that may most rapidly colonise free space. Faster growing corals are also more susceptible to cyclones and bleaching events (e.g. (Marshall and Baird 2000; Carpenter et al. 2008). When preferred faster growing corals are reduced to low abundance, COTS will consume non-preferred slower growing species (Pratchett 2007). Culling COTS is most likely to support the short-term recovery of faster growing corals. The primary sources of coral mortality on the GBR are coral bleaching, COTS and cyclones (De'ath et al. 2012). Modelling how corals interact with each other, as well as cyclone and bleaching disturbances, is important to modelling the efficacy of culling under disturbances; culling may increase coral cover, but this may be quickly lost under other disturbances.
COTS management interactions Removals modelled as a function of age-dependent detectability, population structure, population	The MICE developed here makes use of data on COTS catch rates and the dive time used to help infer COTS densities. Catch rates need to be treated with care because COTS often aggregate which can bias density estimates.

CCIP MICE	Rationale and justification
density, non-linear relationship between COTS density and catch rate, and effort expended at a site. Together these informed the number of COTS removed from given age classes.	Recent studies support that COTS control has a different impact on different age classes and that the relationship between COTS density and catch rates is not linear (e.g. MacNeil et al. 2016; Plagányi et al. 2020; Westcott et al. 2020). Recent data detailing how long Control Teams spent at a site, what their catch rates were, and how many COTS were culled required expansion of the relationship between COTS density and culling efforts. Expanding the relationship to include time also allows for trade-offs to be assessed between how long sites take to control and the impact those efforts have on coral cover.
COTS predator terms • Predators implicitly included in mortality terms but with the option to now explicitly include it given development of fish-predator sub-model as part of this project.	Given several recently identified potential fish predators of COTS are also fishery species (Kroon et al. 2020; Kroon et al. 2021) we were able to source some data from stock assessments published by the Queensland Department of Agriculture and Fisheries (QDAF) to support a generalised fish group for future modelling. The Morello et al. (2014) MICE has been used to explore the possible role of predation in COTS dynamics. They found that predation (unless exceedingly high) is only likely to play a marginal role in COTS population dynamics (for ages-1 and 2+). Predation on early life history stages (age-0) could play a large role but it is unclear how this might vary within and between reefs (an open question with few known predators and how they spatially vary). It was therefore assumed that fitted recruitment and mortality rates implicitly captured the role of predation on age-0 COTS.
COTS prey-switching term • Logistic switching function	Scaling parameter/relationship for the effect of COTS predation on coral cover of a given group. Revised from previous exponential form because the logistic formulation was specified on a range of 0 to 1. The exponential formulation did not range from 0 to 1.

2.3 Data

2.3.1 COTS Control Program

The COTS Control Program data from May 2018 through to July 2021 was made available through the CCIP for model fitting purposes. Data included the dive time at visited reefs and the number of COTS culled. Data were aggregated to the voyage level for a given site (e.g. dive time was the time spent at a site across the voyage). CPUE were computed by dividing the COTS removed by the dive time spent culling them (COTS.min^{-1}). Not all reefs were culled and on reefs that were culled, data were not available for all sites thus the culling data we fitted to did not always have complete coverage of reefs or even within reefs.

2.3.2 COTS Control Program manta tows

The COTS Control Program manta tow data provided individual (non-aggregated) observations of COTS observed, feeding scars, hard coral cover, soft coral cover, and recently dead coral. As manta tows cover a smaller area (approx. 200 m x 10 m) than defined COTS management sites (500 m x 200 m) and do not necessarily travel strictly within sites, multiple manta tows may correspond to a given management site. Manta tows were attributed to their nearest site via an expanding net centred on the management site. To mitigate incorrect manta tow-management site attributions, it was deemed that any site attributed to more than four manta tows was potentially erroneous and discarded. An upper bound of four manta tows per site was considered a realistic number that would minimise incorrect attributions given the operation of the COTS Control Program (Sam Matthews, Dave Williamson pers comm.). Only hard coral cover estimates were used from the COTS Control Program manta tow data as COTS feeding scars were not considered adequately informative of COTS density (Fletcher et al. 2020) and manta tows were considered to provide little information on smaller COTS (Plagányi et al. 2020). Data ranged from November 2018 to June 2021. Further details on how the manta tow coral cover data were used in the model are provided in Appendix A.

2.3.3 Reef Health Impact Surveys

Reef Health Impact Surveys (RHIS) were included as supplementary information to complement the coral data obtained from the COTS Control Program manta tows. RHIS measure coral cover, coral composition, location, habitat, and likely COTS impacts on corals within 5 m diameter plots (approx. 80 m^2). This is much smaller than the area covered by COTS management sites (10 ha = 100,000 m^2) or manta tows (0.2 ha = 2,000 m^2) however the RHIS data was considered to have complementary coral information to the primary manta tow source. RHIS sites proved beneficial because their small size meant they could be directly attributed to a management site, there could be multiple RHIS within a management site to capture variability (or lack thereof), and coral composition was recorded (based on morphology) unlike the manta tows where corals were classified as hard or soft. Further details on how the RHIS coral cover data were used in the model are provided in Appendix A.

2.3.4 Reef selection

The coral-COTS MICE was built up in a stepwise fashion. The first iteration of the model was fitted to four reefs and 13 sites. We then expanded the model to include additional reefs and sites. Additional reefs were shortlisted for inclusion if they had at least six control visits over the period 2018–2021 (see Appendix B). This resulted in a total of 28 reefs and 234 sites. However, insufficient data meant that it was not possible to fit the model to all reefs and sites and the model failed to reach convergence. As a result, only sites with at least 12 control visits were included and the final modelled reef list included 30 sites across 8 reefs (**Figure 4**).

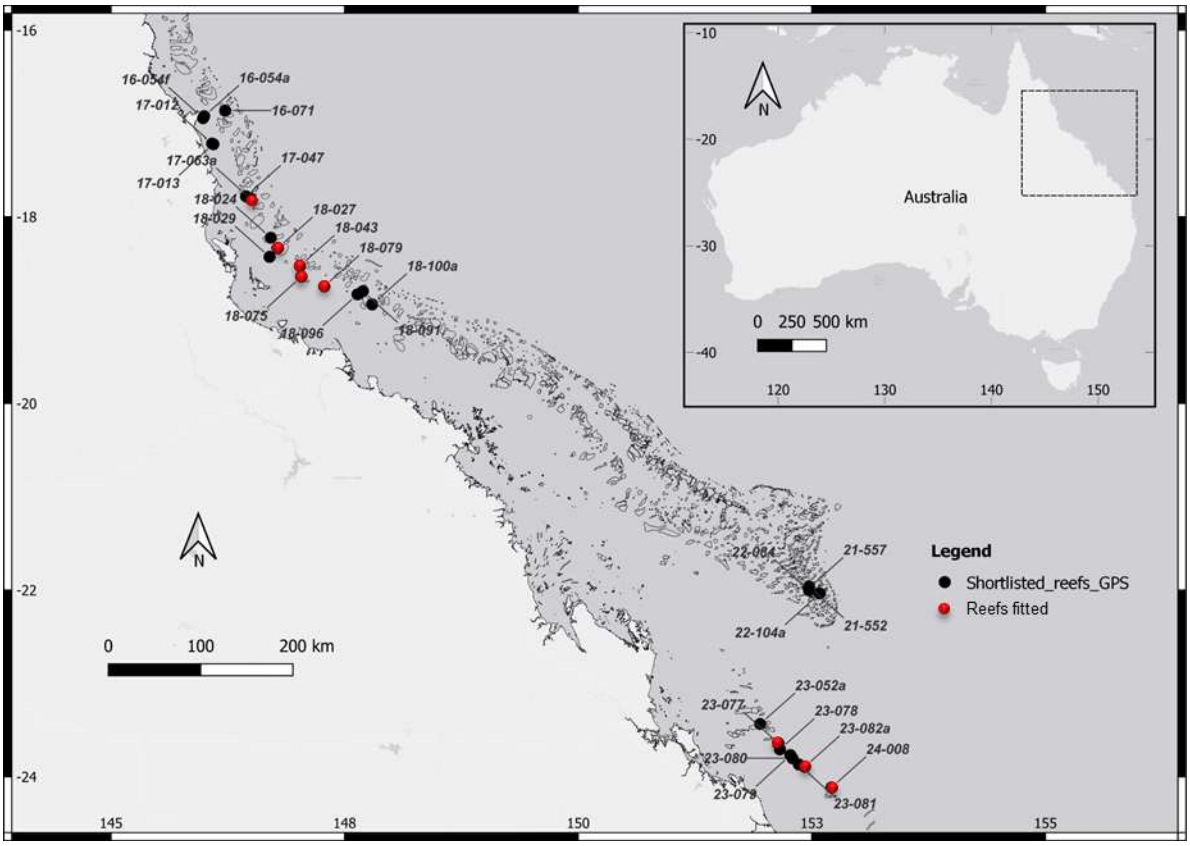


Figure 4. Delineation of reefs successfully fitted in the model (red dots) as well as initial shortlisted reefs for which there were insufficient data (black dots). Inset figure (top right corner) denotes location of finer resolution map (dotted rectangle). Developed in QGIS with the Great Barrier Reef features dataset (GBRMPA 2007).

2.3.5 Potential non-COTS perturbations

COTS are one source of mortality on coral reefs. Other leading causes of coral mortality are severe storms and cyclones as well as coral bleaching (De'ath et al. 2012). To identify potential sources of coral mortality that were not COTS related, the AIMS data portal (https://apps.aims.gov.au/reef-monitoring/reefs) was used to identify whether cyclone(s) and/or bleaching event(s) had occurred at a reef between 2018 and 2021 that would need to be accounted for and attributed during model fitting (see Appendix A for further details).

2.3.6 Fish predators

Data on fish predators of COTS were collated to allow for the development of a model framework that could be used to consider predator-linked COTS behaviour in future modelling. Red-throat emperor (*Lethrinus miniatus*) is an important species for commercial, charter, and recreational fishers in the GBR Marine Park and along the adjacent east Queensland coast from ~18°S to 24°S (Brown et al. 2020; Northrop and Campbell 2020).

Most catches since 1990 have been recorded in the Townsville, Swains, and Mackay regions respectively with relatively limited catches in the Cairns and more northern regions (QDAF, https://qfish.fisheries.qld.gov.au/). Red-throat emperor is a key species in the Reef Line Fishery of the GBR and formal stock assessments for the species have been conducted by QDAF (Leigh et al. 2006; Northrop and Campbell 2020). These assessments consider the region to have a genetically homogenous population. Red-throat emperor can (and do) move between reefs but are thought to be mostly site-attached and are generally found on mid- and outer-shelf reefs (Northrop and Campbell 2020).

Spangled emperor (*Lethrinus nebulosus*) are caught secondarily within the commercial Reef Line Fishery. They are however targeted as a primary species by charter and recreational fisheries (Walton et al. 2021). Most GBR catches for spangled emperor since 1990 have been reported from the Cairns and Townsville regions (QDAF, https://qfish.fisheries.qld.gov.au/). Spangled emperor are currently classified at medium risk under current Tier Ecological Risk Assessment and this is mostly due to the overlap of their range with fishing effort, the likelihood they will successfully be caught by deployed fishing gear, and their likelihood of surviving said interaction (Walton et al. 2021).

2.4 Model fitting

Model fitting was conducted through Maximum Likelihood Estimation (MLE). MLE is a widely used approach to fit dynamical statistical models (e.g. Plagányi and Butterworth 2012; Blamey et al. 2014; Tulloch et al. 2018). It is a versatile method for combining multiple data (e.g. different data sources and/or types) whereby an assumption is made about how the data are distributed about their respective means and the fitting routine weights its inferences from said data based on the variance of each source. For example, a data source with less variability is weighted as more reliable than one which has high variability given the model structure. The likelihood contributions from each source are combined into an objective function which is optimised to find parameter values that maximise the likelihood of the data given the model. Penalty terms may also be included to integrate prior knowledge, or additional systems knowledge into the model fitting. The CCIP MICE is fitted here to data (years 2018–2021) from (1) the COTS Control Program, (2) the COTS Control Program manta tows, (3) and RHIS. Full model details are given in Rogers and Plagányi (2022) while any new equations and likelihood formulations are specified in Appendix C.

CPUE (COTS.min^{-1}) and effort (dive time, min) were used to compute likelihood contributions for the objective function. The likelihood contributions were the primary way in which information on COTS (and management impacts) informed the model dynamics. Reciprocal forcing from coral availability on COTS mortality rates also informed COTS dynamics. CPUE rates from the model and data were used to calculate likelihood contributions from a log-normal distribution. Dive time from the data was treated as an input to the model-predicted CPUE rates to yield modelled catches. A penalty term was included in the objective function to integrate total COTS caught into the model fitting process. This was such that deviations from unity between model estimated catch and observed catch data penalised the parametrisations that yielded them so that the model parametrisation at the MLE gave plausible catch numbers. Recruitment variability was fitted within the CCIP MICE and a penalty term was included to limit extreme fluctuations. Without such a penalty term, too much flexibility is permissible, and this can lead to poor estimation of other model parameters. Both penalty terms were computed based on deviations being normally distributed about either 1 for the catch magnitude penalty, or 0 for the recruitment residuals penalty.

To fit coral cover within the model we considered both manta tow observations and RHIS observations. The manta tow observations provided information on total coral cover and the RHIS observations provided information on coral composition. The model includes two representative coral groups (fast- and slow-growing corals) with COTS generally preferring fast-growing corals relative to slow-growing corals. The model considers potential coral habitat, and that total coral cover is the sum of slow-growing and fast-growing coral cover (i.e. non-suitable habitat is not modelled). Manta tow coral observations were compared with modelled total coral cover to obtain likelihood contributions to the objective function. The RHIS data partitions corals into multiple groups depending on their morphology and these were attributed to either the fast- or slow-growing model groups based on their growth rates and palatability to COTS (see Appendix A). Examination of the aggregated data indicated that trends in total coral cover (from RHIS) was predominantly due to fast-growing corals in the time series. Consequently, only likelihood contributions based on fast-growing corals were included within the objective function based on the RHIS data. Likelihood contributions were calculated based on the deviations between manta tow coral cover observations and model predictions based on a log-normal distribution. The contributions arising from comparing the RHIS fast-growing coral observations with their model equivalents were similarly calculated.

2.5 Refining equilibrium thresholds

2.5.1 Derivation of equilibrium thresholds

The current equilibrium thresholds (**Table 1**) that are used to inform the ecological management thresholds for manual COTS control on the GBR are based on numerically solving equations in Morello et al. (2014) to obtain approximations of the point at which COTS-coral interactions and associated impacts balance coral growth (Plagányi et al. 2020). This entails equating the population dynamics of aggregated coral groups (e.g. fast-growing or slow-growing) to the effects of COTS-coral feeding interactions. Further details are provided in Appendix D and Rogers et al. (2024).

2.5.2 Sensitivity of equilibrium thresholds to variation in coral growth rates

Given that coral growth varies along the extent of the GBR, and may also vary following bleaching events, we investigated how differences in coral growth rate parameters influenced coral growth-COTS predation interactions. For fast-growing corals we modelled variation of growth parameters to account for a 0 % to 70 % reduction in growth rates. Under the assumption that slow-growing corals were less susceptible to thermally-induced variation in their growth rates, we modelled more coarse growth reductions ranging from 0 % to 40 %. This was computed at different levels of fast-growing coral (i.e. fast and slow-growing corals compete for space). In addition to potential reduced growth rates, we also modelled small increases (10 % and 20 %) in the growth rate of fast-growing corals.

Keesing and Lucas (1992) measured in situ feeding rates of COTS at Davies and Little Broadhurst Reefs (south of Lizard Island) and used these to estimate COTS densities (of age-2+ equivalent COTS in our model framework) that would have limited impact on corals. We tested growth rates to approximate the specified outbreak density of 10 COTS.ha^{-1}

(Keesing and Lucas 1992) (8.2 COTS.ha^{-1} when accounting for 82 % age-2+ detectability) which corresponded to a ~65 % increase in the modelled growth rates of coral. Hence, a 65 % increased growth rate sensitivity was modelled for both fast- and slow-growing corals. Visualisation of different coral growth rates induced by given changes are provided in **Figure 5** so that subsequent thresholds can be linked to reefs (or regions) where the intrinsic growth rate of coral populations is known or could be inferred.

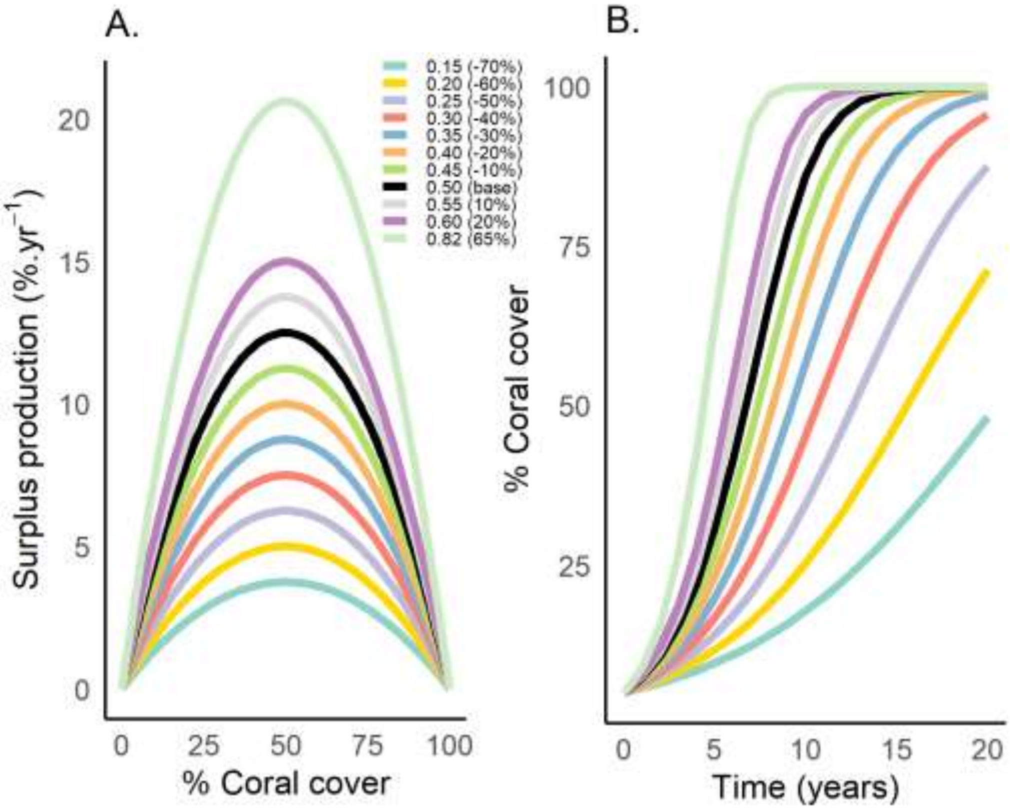


Figure 5. Alternative growth rate scenarios considered by Rogers et al. (2024). Legend provides the intrinsic growth rate simulated and the relative difference to the base growth rate is in brackets. **(A)** surplus production curve for a given growth rate change at a given level of coral cover. **(B)** coral recovery curve for a given growth rate from an initial depletion level of 5 %.

2.5.3 Translating thresholds to catch rates

The relationship between true COTS density at a site and the expected catch rate of individuals at the location is not linear (Babcock et al. 2014; MacNeil et al. 2016; Plagányi et al. 2020) and can vary due to several factors. Search and handling time, COTS population density, detectability, and available dive time are accounted for through a hyperstability relationship (see Plagányi et al. 2020). The approach to defining equilibrium thresholds relies on numerically finding the expected annual change in coral cover from a COTS population of a given density (COTS.ha^{-1}). The COTS density is then used to compute the expected CPUE based on the non-linear hyperstability relationship of Plagányi et al. (2020) which involves inferring the density of age-1 COTS given the density of age-2+ COTS numerically found to result in a given change in coral cover. The analytical estimate of age-1 COTS density relies on annual COTS mortality rates and the threshold value CPUE depends on the detectability of both age-1 and age-2+ COTS. Sensitivity of COTS mortality is examined by simulating a higher mortality rate. Sensitivity to COTS detectability by control divers is examined by increasing the detection rate of age-1 COTS. Both mortality and detectability were considered simultaneously. Assumed detectability and mortality rates were based on the alternatives suggested by Plagányi et al. (2020) and included the consideration of 19 % (base case) or 34 % detectability of age-1 COTS and a mortality rate of either M=2.56 (base case) or M=1.76. Spatial resolution is implicitly that at which culling numbers and time are reported (e.g. “site level” ~10 ha). Further details are provided in Appendix D.

2.5.4 Considering demographic uncertainty in catch rate metric

Estimates of COTS population densities are notoriously variable, in part due to the differential detectability across ages (and corresponding sizes) and demographic skews within a population. COTS populations with different age compositions, different detection rates, and different mortality rates could impact recommended CPUE values; the influence of these factors on CPUE thresholds was therefore investigated. Equilibrium population dynamics are a demographic (analytical) tipping point between population growth and decline. These tipping points were visually represented (**Table 3** and **Table 4**) in terms of currently used management CPUEs arising from a population of age-1 (on vertical axis) and age-2+ (on horizontal axis) COTS where diagonal lines (from plot top left towards bottom right) correspond to different mortality rates. Populations below an equilibrium line suggest that the age-1 cohort could be of sufficient size to subsequently increase the ensuing age-2+ cohort. Conversely, populations above the equilibrium line indicate that there are possibly too few age-1 individuals to sustain the age-2+ population and that, with time, the size of the age-2+ cohort may decrease. These CPUE values for different population compositions were then compared against the “ecological management threshold” and the CPUE proxy of the “fertilisation threshold” to infer their generality across differently structured COTS populations.

2.6 Comparison of IPM and past or no intervention strategies

We codified the current IPM (implemented from 2018 onwards) for comparison to the implemented historical (2013–2018) method and a no-control scenario from 2013 to 2018, to evaluate whether a more formalised operation would have provided better outcomes for the management objective of culling COTS down to “threshold levels that promote coral growth and recovery” (GBRMPA 2023) for that time period. The simplified decision tree (**Figure 6**) used as part of the operational strategy for COTS control (Fletcher et al. 2020) was, for the first time, coded for simulation within the COTS MICE. The inclusion of the decision tree within the model allows for inferring how COTS control thresholds interact with observation, detection, and implementation uncertainties, the strategy within which they are deployed (for a set of reefs), and the time scale with which they are deployed— something not previously available in the suite of COTS models and which is considered best practice in fisheries approaches (e.g. see management strategy evaluation; Punt et al. 2016). The MICE was fitted to the COTS control CPUE data and total coral cover data starting in June 2013 up to July 2018. The model was fitted to 13 management sites that were distributed across four different reefs. All reefs were in the vicinity of Cairns. The timeframe and geographical location of the ‘study’ sites meant that reefs were subject to the back-to-back bleaching events of 2016 and 2017 (Hughes et al. 2019a). Not all reef sites were impacted the same and the consequences for corals varied between sites (Rogers and Plagányi 2022). Further details are provided in Appendix E.

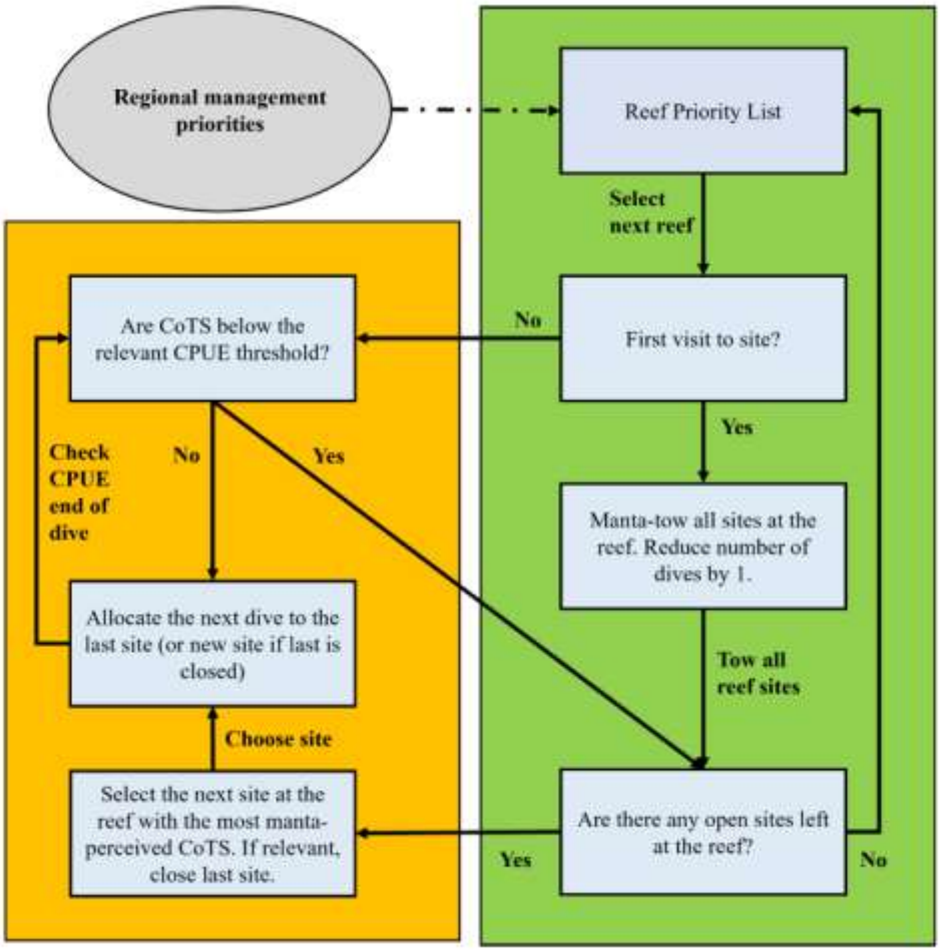


Figure 6. Implemented decision tree algorithm for crown-of-thorns starfish (COTS) Model of Intermediate Complexity for Ecosystem assessment (MICE). Decision tree is based on the simplified decision tree for on-water COTS control (Fletcher et al. 2020). Grey circle: Regional management priorities determine the reefs that form the priority list circulated for on-water COTS control (not modelled). Blue boxes: Decision or action points; decision points specify the key question that must be answered. Green box: Decision and actions underpinned by manta tow information on COTS and coral distributions. If no reefs are identified as needing COTS control, then the green box ends up conducting reef surveillance based on manta tows. All reefs in the priority list are cycled through. Orange box: If a reef is detected by surveillance as needing control, then the site at the reef with the highest manta tow-detected COTS density is selected. If no dives have been conducted at the selected site, a dive is conducted. For sites that have been previously dived, manta tow data is replaced by catch-per-unit-effort (CPUE) data. The CPUE achieved on each dive is compared to the relevant management threshold to inform whether further dives at the site are required. If the CPUE is below the threshold, then the next site with the most COTS (as informed by the initial reef manta tow) is selected for control. If all sites are below the threshold (closed), then the green box is re-entered to identify the next reef on the priority list. The orange box ensures that a site is controlled to below threshold levels before a new site is controlled; all sites at a reef are controlled before a new reef is selected.

The MICE was expanded to increase spatial coverage (8 sites and 30 reefs, see section 2.2) and was fitted to data from the current COTS Control Program (2018–2021). This model was then used to examine the efficacy of the current COTS Control Program to improve coral cover at the site level. The fitted model was used to create a model-based counterfactual to the fitted trajectories by setting to 0 the time spent culling COTS at each site for years 2018 to 2021.

2.7 Accounting for predation risk to COTS: Expanding model framework for simulating future management strategies

Predator release has been hypothesised to be involved in the initiation and propagation of population irruptions (or 'outbreaks') of COTS (*Acanthaster cf. solaris*; e.g. Ormond et al. 1990; Dulvy et al. 2004; Cowan et al. 2017). Recent DNA-based analysis of fish faeces has strongly suggested that two species, red-throat emperor and spangled emperor, both of which are subject to fishing pressure on the GBR consume COTS (Kroon et al. 2020; Kroon et al. 2021). Moreover, comparing the likelihood of COTS outbreaks on a reef with the reef area's retained fisheries catches also suggests, that in places of higher exploitation, outbreak occurrence is higher (Kroon et al. 2021). A similar finding has been observed by others whereby areas in which fishing is restricted often have fewer outbreaks and lower COTS densities (Sweatman 2008; Westcott et al. 2020). Both red-throat and spangled emperor have been historically fished on the GBR and identified as likely COTS predators (Cowan et al. 2017; Kroon et al. 2020; Kroon et al. 2021) (noting that preliminary results presented from CCIP-P-06 (Doll et al. 2025) indicate support for spangled emperor as a potentially important predator). Hence, we selected the two species as candidates to represent the role of fish as COTS predators in the coral-COTS model.

A Schaefer production model was used to model fish, given the availability and type (biomass) of data, and the generality and robustness of the formulation. The shape of the production curve within the Schaefer model is quadratic. We note that this formulation conflates exploitable and spawning biomass, does not factor restrictive measures (e.g. size limits), and is a simple representation that allows for more tractable mathematics to reasonably represent the species in an ecosystem model for coral and COTS dynamics.

For red-throat emperor, a standardised abundance index (Northrop and Campbell 2020) was used to estimate the intrinsic growth rate for the model (r). There was insufficient contrast in the data to estimate both the growth rate and carrying capacity, K, and attempts to do so resulted in near linear correlation between the parameters. As K is scale dependent, the data is at whole-of-GBR scale, and we wanted to model fish as predators at the reef scale, we instead chose to estimate r. It is important to note that because we forced the submodel with catch data and specify K, then the population depletion level (P_y/K) is also dependent on K and so is not reflective of actual stock status. We fixed $K =$ 12,000 t and conducted a sensitivity analysis for $K =$11,000t, 13,000t. The Schaefer model is given by:

$$P_{y+1} = P_y + r \cdot SR \cdot P_y \cdot \left(1 - P_y\right) - \frac{C_y}{K} \qquad [1]$$

For spangled emperor, we did not have a reliable abundance index to fit the model to (e.g. standardised CPUE data), so it was not possible to estimate parameters. We therefore assume generality of the red-throat emperor Schaefer model.

For a given number of potential fish predators ($P_{y,d}^{Rf,i}$) and vulnerable COTS of age-*a* in management site-i ($N_i^{exp,a}$), COTS can be modelled to be consumed proportional to their availability. The number of exploitable COTS is linked to local coral availability and COTS preference to exhibit searching behaviour given predator risk (e.g. as per Appendix D: Equation D.4). Predation rates on COTS are here suggested to be modelled as a decreasing function of local COTS density (type II functional response) consistent with the saturation of predators or strong handling time constraints (McCallum et al. 1989). Predators were assumed to have a selectivity for age a individuals of S_a^{φ}. The predator consumption rate can therefore be calculated by:

$$Q_{y,d,a,i}^{CoTS} = \frac{p_1^{CoTS} P_{y,d}^{Rf,i}}{1 + e^{-\sum_{k=1}^{3+}\left(S_a^{\varphi} N_{y,d,i}^{exp,a}\right)/p_2^{CoTS}}} \qquad [2]$$

Parameters p_1^{CoTS} and p_2^{CoTS} respectively denote the maximal consumption rate of COTS by predators and the rate at which the predator consumption of COTS saturates. The selectivity (S_a^{φ}) of age-1 and age-2 COTS can be taken to be 1 (note that here selectivity is a coefficient of those left after cryptic/non-accessible individuals have been removed, i.e. available COTS). Large age-3+ COTS are assigned zero selectivity because they are sufficiently large to escape predation. This selectivity assumption is consistent with differences in behavioural patterns (De'ath and Moran 1998; Burn et al. 2020) as well as observed sublethal predation (McCallum et al. 1989; Rivera-Posada et al. 2014a).

2.8 Stakeholder engagement

Key stakeholders of this reef-scale modelling project include the Great Barrier Reef Marine Park Authority (GBRMPA), COTS Control Program on-water operators and other CCIP researchers. Below we summarise engagement that has taken place during this project.

2.8.1 GBRMPA

- Discussion of CPUE values around targeting of the fertilisation threshold. Current control activities are achieving low CPUE values consistent with the estimated CPUE value for the fertilisation threshold. There is interest to develop a workflow algorithm for the CPUE fertilisation threshold for integration into the COTS management dashboard to help identify where COTS control has likely achieved the fertilisation threshold. This could help understand the role of the fertilisation threshold in broader (regional) outbreak dynamics.
- Discussion of the retrospective efficacy of COTS control over 2013 to 2018 (pre-IPM approach) presented in Rogers and Plagányi (2022). There was interest in testing the efficacy of current control procedures to compare with historical outcomes. The project team incorporated this request by running the simplified decision tree of Fletcher et al. (2020) over the years 2013 to 2018 to compare with the intervention that took place over that time.
- GBRMPA requested that additional reefs were included in the CCIP MICE model.
- Discussion around coral and COTS data with GBRMPA and the modelling of likely coral trajectories without COTS control intervention and the possibility of modelling this using the updated model.
- Discussion with GBRMPA around Effort Sinks (see Appendix F for definition).
- Discussion with GBRMPA about moving towards a single threshold in the future.

2.8.2 COTS Action Group

- Our team presented some of the early results from this project to the COTS Action Group. Specifically, the team presented how growth rates impact CPUE thresholds and the translation of the fertilisation threshold (a density-based metric) into a CPUE value. This information was well-received and given time constraints, noted that further discussion was needed. The COTS Action Group provided insight into how data are collected and how this relates to achieved CPUE values on water. General agreement that it would be beneficial for CCIP groups (ours and others) to connect with the Action Group to discuss their work and how this relates to on-water control. Agreement that further engagement with on-water operators and GBRMPA would be beneficial.

2.8.3 CCIP researchers

- *Prediction subprogram*: The project team met with project leads from the Prediction subprogram in February 2021 to discuss timelines of field- and lab-based projects and data that would potentially be available to inform the model in CCIP-R-03 (Rogers et al. 2025). Projects that were identified as most likely to inform modelling in CCIP-R-03 (and similar efforts in future) were CCIP-P-01 (Pratchett et al. 2025a), and CCIP-P-06 (Doll et al. 2025). Work quantifying predation rates (CCIP-P-06, Doll et al. 2025) was expected to produce results at individual level and some consideration was needed on whether and how this could be extrapolated to population level as required for our model. At a minimum, a proxy of predation rates (green vs blue zones) would be able to be provided at the end of the CCIP. Potential for information from projects looking at in situ feeding rates (CCIP-P-01, Pratchett et al. 2025a) and population collapse (CCIP-P-02) to also inform COTS dynamics in the model was considered. It was discussed how CCIP-R-03 (Rogers et al. 2025) could feed back to Prediction subprograms and provide information on data gaps or model sensitivities and how field or lab-based studies, or expert knowledge, could help resolve this. It was deemed unlikely that data would be available. The R-03 project team followed up in August 2022 with (previous) project lead Ciemon Caballes to discuss progress on field-based projects, specifically CCIP-P-01 (Pratchett et al. 2025a), CCIP-P-02 (which was terminated), CCIP-P-04 (Pratchett et al. 2025b) and CCIP-P-06 (Doll et al. 2025) and what data may be available when these projects were completed and whether study sites overlapped with modelled sites. Ciemon was also able to give a summary of some initial findings from his work in Guam. We were able to provide Ciemon with an update on the modelling project and what would be included in the next steps (framework for movement, behaviour, predation) and get his expertise/knowledge to help underpin some of the model framework being developed. There were also ongoing discussions with Morgan Pratchett regarding Torres Strait COTS monitoring and some of the work that was being conducted as part of CCIP-R-03 (Rogers et al. 2025). Morgan shared Scooter Assisted Large Area Diver survey (SALAD) COTS density data and coral composition data.
- *Detection subprogram*: Our team had discussions with Scott Bainbridge and Brano Kusy about validation of the manta data vs the transom coral cover data and the possibility of quantifying the variability associated with the ordinal categories used in the manta-based coral cover surveys. We also attended CCIP CSIRO meetings led by Emma Lawrence in 2023.
- *Response subprogram*: Our project team had ongoing discussions with other modelling groups including discussion with Russ Babcock regarding modelling of coral groups; discussion with Scott Condie regarding modelling predators; and discussion with CSIRO, UQ and JCU researchers on Effort Sink reefs in July 2023.
- *CCIP-wide workshops*: The project team attended and participated in all three CCIP workshops (October 2022, May 2023 and November 2023). Here we were able to share

project updates and draft results as well as connect with the COTS Control Program (on-water operators), GBRMPA and other CCIP project leads.

- Jacob Rogers gave the first seminar in the CCIP seminar series in February 2023 where he presented an overview of current CCIP work to the wider CCIP community.
- Jacob Rogers, Laura Blamey and Eva Plagányi attended the Modelling Decision Support (MDS) & Data Management Support (DMS) Alignment and Integration Workshops 1 (26 April 2023) and 2 (8 May 2023). Jacob Rogers presented an overview of MICE models and how they have been used on the GBR to inform COTS-coral interactions.
- Laura Blamey attended the Reef Resilience Symposium in April 2024 and presented some of the results from this project.

2.8.4 Other

- Jacob Rogers and Laura Blamey attended the Australian Marine Sciences Association (AMSA) symposium in August 2022 in Cairns and had the opportunity to connect with other CCIP researchers and GBRMPA. Jacob Rogers presented an update of current CCIP work “MICE to inform COTS control, effort sinks, and model-based support of the COTS decision tree approach for reef and site selection”.
- Eva Plagányi, Laura Blamey, Jacob Rogers and Cameron Fletcher attended a CSIRO cross-domain ecosystem modelling workshop in Canberra, 11 May 2023. Eva and Laura presented an overview of MICE modelling with reference to the CCIP modelling on GBR.
- Jacob Rogers attended a training workshop at University of Washington in September 2023 and presented a guest seminar providing an overview of MICE models and how they have been used on the GBR to examine COTS-coral interactions.
- Eva Plagányi and Nicole Murphy attended the 3rd meeting of the Hand Collectables Resource Assessment Group (HCRAG03), 17–18 October 2023, Waibene (Torres Strait) and shared information about our COTS research and historical data to complement discussions and feedback from the Torres Strait Regional Authority (TSRA) regarding management of COTS in the Torres Strait. Ongoing discussions with Torres Strait Traditional Owners and stakeholders re COTS management.
- Jacob Rogers, Éva Plagányi and Laura Blamey attended AMSA 2024 in Hobart. Jacob Rogers presented outcomes from CCIP-R-03 (Rogers et al. 2025).

3. RESULTS

3.1 Refining equilibrium thresholds

3.1.1 Balancing COTS predation effects and coral growth: Equilibrium dynamics and thresholds

Analysis indicates that the threshold of Keesing and Lucas (1992) of 10 COTS.ha^{-1} (8.2 COTS.ha^{-1} when adjusted for 82 % detectability) is substantially higher than the equilibrium levels that balance the effects of COTS predation and coral growth (**Figure 7a**). Under the base case parametrisation (Plagányi et al. 2020), the MICE suggests the coral-COTS equilibrium threshold is up to 10 COTS.ha^{-1} lower depending on fast-growing coral cover (under the assumption that Keesing and Lucas (1992) were targeting comparable COTS to our age-2+ size class).

At low cover of fast-growing corals (0 % to 20 %), differences in coral growth rates relative to the base parametrisation resulted in a difference of ~1–2 age-2+ COTS.ha^{-1} supported by corals (**Figure 7a**). At high coral cover (~80 %), differences in coral growth relative to the base parametrisation amounted to substantial differences in the number of COTS supported (**Figure 7a**). As the growth rate of preferred fast-growing corals was reduced (from 0 to -70 %), the number of potential age-2+ COTS supported dropped by up to ~10 COTS.ha^{-1}.

Growth reductions (0 % to -70 % relative to base case) amounted to at most a difference of ~0.04 COTS.min^{-1} in CPUE (**Figure 7b**). At 30 % fast-growing coral cover, the difference was ~0.02 COTS.min^{-1}. Over the range of 0 % to 20 % coral cover, the differences in CPUE owing to differences in coral growth were ~0.01 COTS.min^{-1}. The fertilisation threshold was below equilibrium levels for base dynamics however overestimated equilibrium levels at low coral cover. For example, this occurred if fast-growing coral cover was low (<10 %) and coral growth was relatively reduced (>30 %) compared to the base parametrisation.

The currently implemented two-tier CPUE targets of 0.04 COTS.min^{-1} and 0.08 COTS.min^{-1} (**Table 1**) suggest coral growth rates would need to be larger than the base case model. Faster growth rates would be needed because the base case equilibrium line (black solid line, **Figure 7b**) is mostly below the two-tier CPUE target (upper dashed red line, **Figure 7b**) so if control stops at the threshold, then coral will likely still be lost. The two-tier CPUE threshold corresponds better to the approximate Keesing and Lucas (1992) 10 COTS.ha^{-1} density threshold (65 % increase in growth rate) because that equilibrium line is mostly above the two-tier CPUE threshold (theoretically avoiding coral loss due to COTS).

The range of different coral growth rates tested – including 10 % and 20 % increases in the growth rate – all suggested that the point at which coral growth was exceeded by the impacts of COTS predation was below 10 COTS.ha^{-1} (8.2 COTS.ha^{-1} adjusted for detectability) and the current CPUE targets of 0.04 COTS.min^{-1} and 0.08 COTS.min^{-1}. It is however critical to note that while the MICE suggests that CPUE thresholds may be above the equilibrium coral-COTS point, the consequence of this in terms of coral cover may not be as severe as initially perceived (subsequently presented in section 3.1.2).

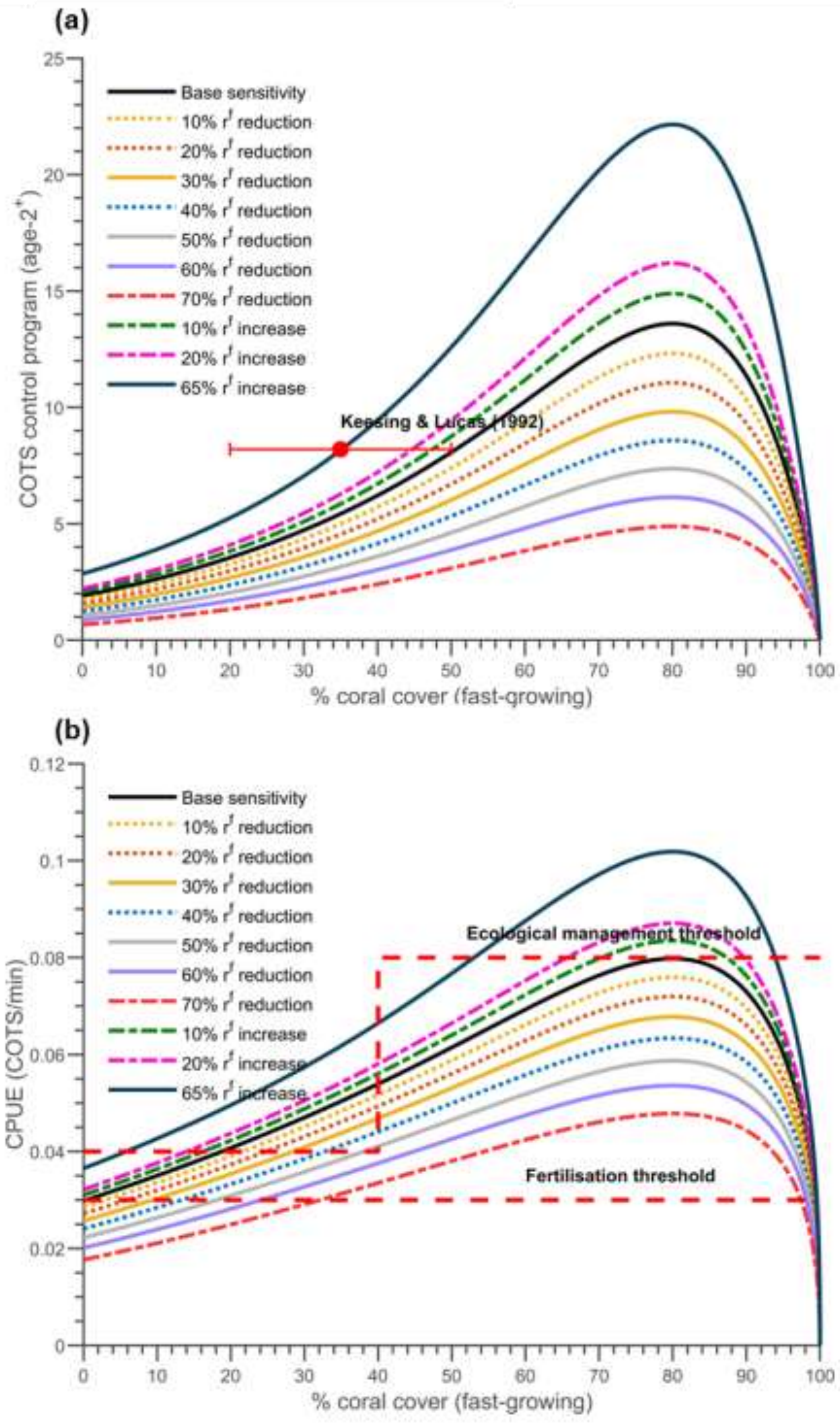


Figure 7. **(a)** Density of age-2+ COTS/ha available (detectable) to the Control Program and **(b)** Expected catch-per-unit-effort (CPUE) for the Control Program against depletion level of fast-growing coral prey. Lines indicate the point at which the effects of COTS predation equilibrate the growth capacity of fast-growing corals. Different line colours and styles indicate alternative coral growth values relative to the parametrisation employed by Plagányi et al. (2020). In panel **(a)**, the derived outbreak density (10 COTS.ha-1) based on coral growth and COTS consumption of Keesing and Lucas (1992) (adjusted for an 82% detection rate) is provided as reference. In panel **(b)** the red dashed lines indicate salient thresholds for COTS control on the GBR. These are the ecological management threshold (based on Plagányi et al. 2020; Babcock et al. 2014) and the fertilisation threshold (Rogers et al. 2017) converted to an expected CPUE here (0.03 COTS.ha-1).

Growth reductions had little impact on the equilibrium levels for slow-growing corals. Growth reductions of 20 %, 30 % and 40 % (Appendix G) had negligible impact on the equilibrium coral-COTS threshold (mostly <0.005 COTS.min^{-1}). Increased growth capacity (65 %) did increase the equilibrium coral-COTS threshold, but this again was only small (mostly <0.005 COTS.min^{-1}) unless the cover of fast-growing corals was very high (fixed at 80 % then ~0.015 COTS.min^{-1}). The capacity to manage to such fine levels was assumed to be impractical and beyond the capacity of current manual COTS control. As such, further analyses were focused on fast-growing corals.

3.1.2 Expected change in coral cover by targeting thresholds: Delineating the prevention of coral loss and improvement of coral cover

The location of equilibrium coral-COTS thresholds (indicated by the nullcline i.e. zero-line) remained similar across the different relative growth rate reductions tested. However, the benefit (in terms of coral cover) of controlling to below the ecological management threshold (**Table 1**) decreases as coral growth rates decrease (**Figure 8**; note Box 1 provides interpretation notes for this report's contour plots). That is, the expected improvement in coral cover by culling to below the equilibrium (nullcline) between COTS predation effects and coral growth decreased as coral growth rates were reduced. Conversely, if growth rates were faster then there was greater potential to improve coral cover through COTS control.

For the base case, the required CPUE for achieving sub-fertilisation threshold densities (nominally 0.03 COTS.min^{-1} for equilibrium dynamics but see **Table 4**) suggests that, if attained, an annual coral cover improvement of +5 % may be possible at the site of control. We explicitly note and emphasise that this is at the site of control and therefore does not incorporate any potential broader benefits for coral cover that may occur as a result of suppressing COTS recruitment within a reef network.

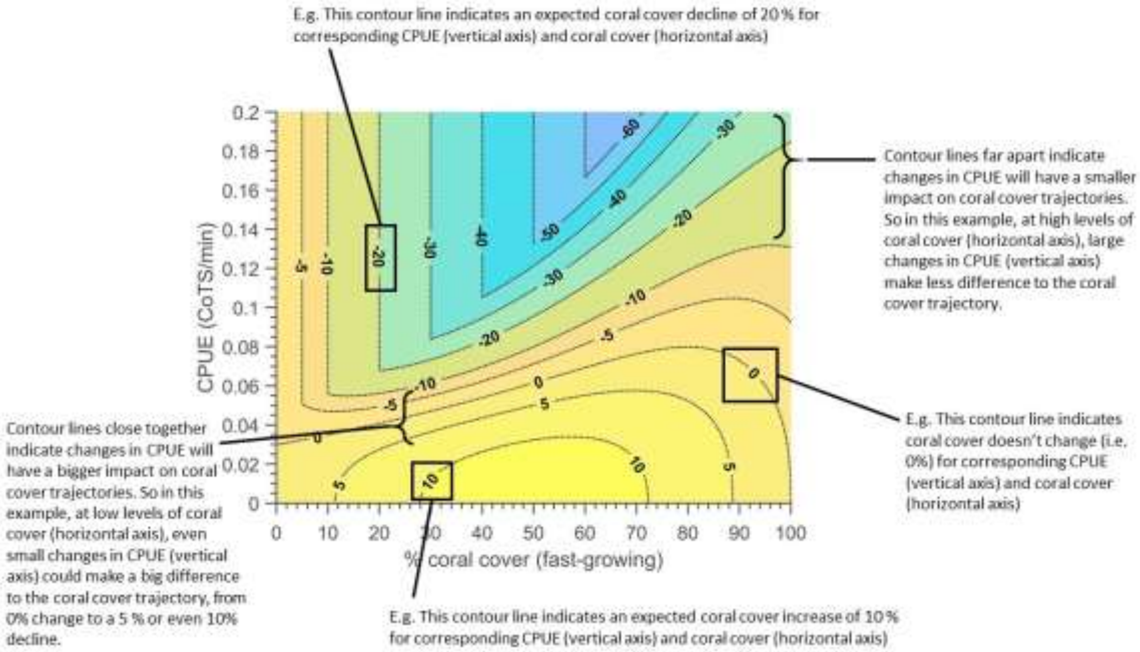
When applying the ecological management threshold of 0.04 COTS.min^{-1} if coral cover is <40 % the base case indicates that this would allow for a 0 % to +5 % change in fast-growing coral cover (**Figure 8a**). If cover is ≥40 % then the model suggests that the target of 0.08 COTS.min^{-1} results in an expected annual decrease in coral cover by 0 % to -7 % with the most drastic predicted losses occurring at the CPUE step of 40 % coral cover. At 40 % cover, losses may be up to ~15 %.

The model suggested that the greatest opportunity for management to not just prevent loss but improve coral cover through manual control occurs at sites with intermediate levels of coral cover (25 % to 55 %) (**Figure 8**). This is based on the closely located contours in the expected change in coral cover as a function of CPUE at such levels (e.g. the base case; **Figure 8a**). With similar justification, above the nullcline, contours are closest from ~20 % to 40 % fast growing coral cover. This indicates that sites with coral cover ranging from 20 % to 40 % are most at risk of rapid coral cover loss if above equilibrium COTS densities persist.

It is worthwhile noting that while reductions in coral growth capacity limited the benefit of achieving densities below the equilibrium threshold, growth rate reductions did not substantially impact coral cover loss when COTS predation effects exceeded coral growth capacity (**Figure 8**). Coral loss at above threshold densities was similar across relative differences in growth rates from an increase of +20 % to a decrease of -70 % relative to the base case parametrisation.

Box 1 Contour plots for understanding COTS CPUE outcomes on coral cover

Contour plots are used to visualise how coral cover may change under different CPUE rates. CPUE is presumed to reflect COTS densities (a proxy). These plots are a way to represent a 3-dimensional surface in 2 dimensions in the same way as a topographic map. Individual lines represent different 'heights' of the surface which are denoted by the number attached to the line (contour lines). Comparing adjacent lines that use a specified increment (e.g. 10 m or 50 m increments on a topographic map) indicates slope of the surface. Differences in contour line numbers represent the 'vertical' difference between them (e.g. difference between 10 m and 40 m contour indicates a 30 m difference on a topographic map). Lines that are close together indicate a steep slope or if lines are far apart, they indicate a gentle slope. In our case increments are coral cover as a function of CPUE. This means that if lines are close together, they suggest changes in CPUE can have a substantial impact on coral cover. Conversely, if the contour lines are further apart then they suggest that changes in CPUE will have a smaller impact on coral cover trajectories. If one wishes to achieve the most impact on coral cover (or avoid the most detrimental impacts on coral cover) then management resources will have the greatest impact where contours are closely located and lesser impact where they are further apart. A nullcline is a contour where no change is expected (difference is zero, null difference).



E.g. This contour line indicates an expected coral cover decline of 20 % for corresponding CPUE (vertical axis) and coral cover (horizontal axis)

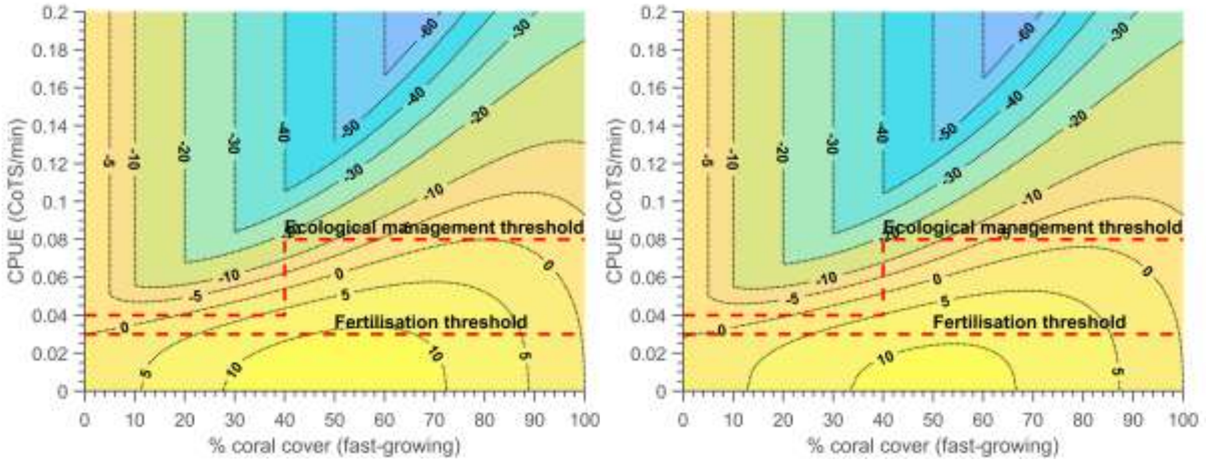
Contour lines far apart indicate changes in CPUE will have a smaller impact on coral cover trajectories. So in this example, at high levels of coral cover (horizontal axis), large changes in CPUE (vertical axis) make less difference to the coral cover trajectory.

E.g. This contour line indicates coral cover doesn't change (i.e. 0%) for corresponding CPUE (vertical axis) and coral cover (horizontal axis)

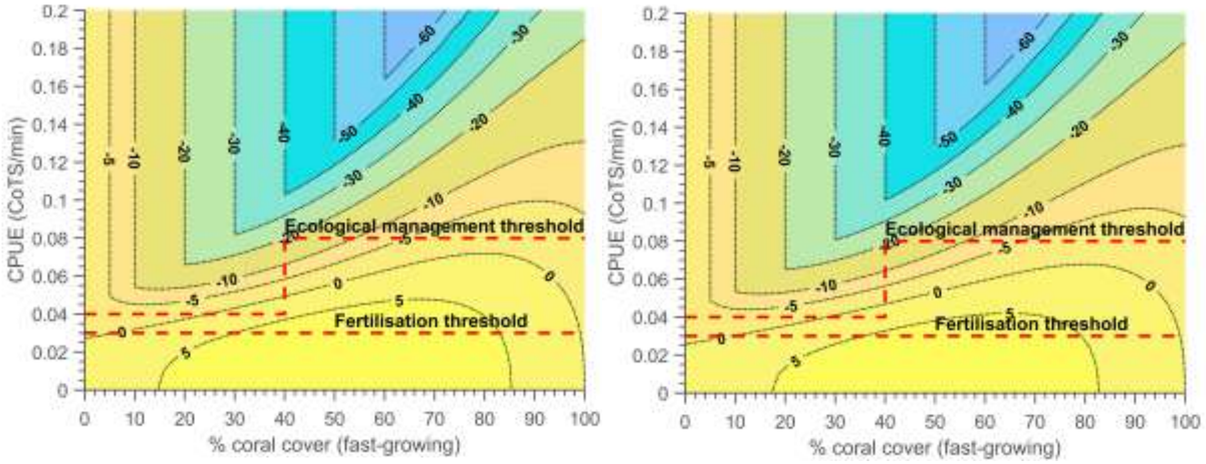
Contour lines close together indicate changes in CPUE will have a bigger impact on coral cover trajectories. So in this example, at low levels of coral cover (horizontal axis), even small changes in CPUE (vertical axis) could make a big difference to the coral cover trajectory, from 0% change to a 5 % or even 10% decline.

E.g. This contour line indicates an expected coral cover increase of 10 % for corresponding CPUE (vertical axis) and coral cover (horizontal axis)

(a) 0 % difference **(b)** 10 % decrease



(c) 20 % decrease **(d)** 30 % decrease



(e) 40 % decrease **(f)** 50 % decrease

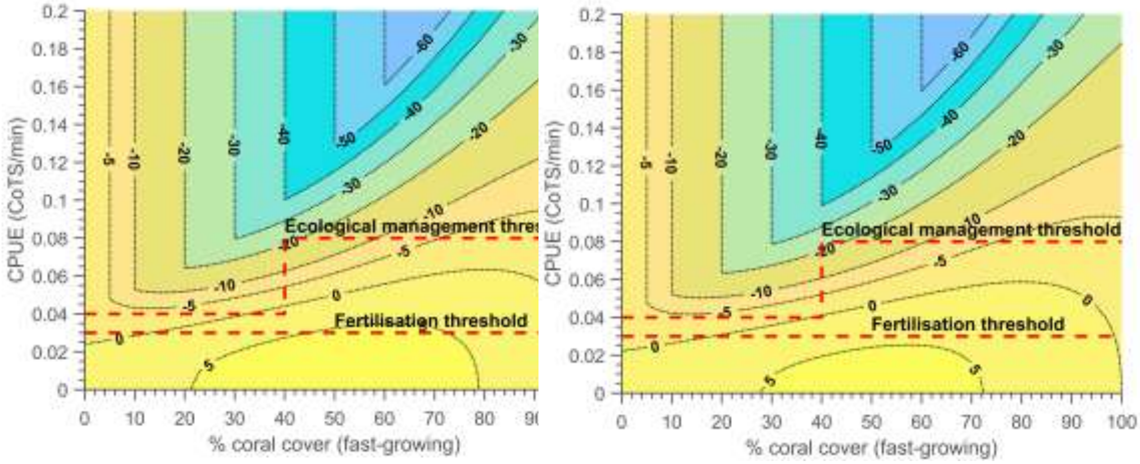


Figure 8. (a) Base case 0 % difference in fast-growing coral growth rate (Plagányi et al. 2020) included here as an index figure for reference, **(b)** 10 % decrease in fast-growing coral growth relative to base case, **(c)** 20 % decrease in fast-growing coral growth relative to base case, **(d)** 30 % decrease in fast-growing coral growth relative to base case, **(e)** 40 % decrease in fast-growing coral growth relative to base case, and **(f)** 50 % decrease in fast-growing coral growth relative to base case. See Box 1 for assistance with plot interpretation.

3.1.3 Considering demographic uncertainty when defining target thresholds

Demographic uncertainty can be thought of as the range of COTS population age compositions that may yield the same CPUE value. If using CPUE to define thresholds around COTS density targets, lower CPUE objectives reduce demographic uncertainty. For example, a CPUE of 0.01 – 0.02 COTS.min^{-1} would better realise an age-2+ 3 COTS.ha^{-1} target (**Table 3**). Alternatively, increased detectability can reduce uncertainty around specific CPUE values (age-1 detectability; **Table 4**). **Table 3** and **Table 4** also highlight the difficulty in estimating demography of a population based on only CPUE as the relationship to density is not one-to-one or linear (see Appendix D equations [D.3] – [D.4]). If effort (dive time), hyperstability dynamics, and catch size-age composition are captured across culling sites (sites ~10 ha), then density estimates at this spatial scale may be possible.

Demographic information about the COTS catch would assist in reducing uncertainty around CPUE thresholds and corresponding COTS density (provided age-class detectability metrics are applicable for the control site). Given base case detection rates (i.e. $\beta = 0.19$) consideration of demographic uncertainty is likely most relevant for detectable populations of <13 COTS.ha^{-1} if using CPUE targets without consideration of catch size composition. Reliable catch composition could allow for better (adaptive) calibration of CPUE targets. If recorded compositions are not deemed reliable (or yet available), for example on the first control visit of a site, then a precautionary CPUE of ~ 0.01 – 0.02 COTS.min^{-1} may be initially applicable. Otherwise, relevant target CPUEs may be approximately gauged based on the size composition of the catch as culling information at the site becomes available (green shaded area; **Table 3** and **Table 4**). This may enhance follow up control specificity and surveillance and monitoring of specific density thresholds, though this should first be evaluated against field control and monitoring data. Monitoring data via video technologies may be useful here.

We note that having a target threshold for each size class would be valuable information to guide COTS culling. To do this would require examining the size structure of culled COTS for a given CPUE and analysing the distribution of COTS sizes that lead to each CPUE measurement. This could then be compared to the equilibrium coral-COTS threshold (diagonal line in **Table 3** and **Table 4**). However, the overall CPUE reflects the culling of differently sized COTS and the contribution of different COTS classes to this will likely retain a level of confounding. What can be done though, is the specification of a conservative CPUE that accounts for how uncertainty in the population size structure impacts the CPUE target threshold. A precautionary target CPUE for the fertilisation threshold would be 0.01 – 0.02 COTS.min^{-1} (the fertilisation threshold is not the current management target). The ecological management threshold currently used (0.04 COTS.min^{-1} for coral cover < 40 % and 0.08 COTS.min^{-1} otherwise) for limiting coral loss is already conservative relative to different age structures and remains fit for purpose (see figures S5–S6 in Rogers et al. 2024). A similarly tiered threshold of 0.04 COTS.min^{-1} for coral cover < 40 %, 0.06 COTS.min^{-1} for 40–60 % coral cover, and 0.08 COTS.min^{-1} otherwise would also be conservative.

Table 3. Expected catch-per-unit-effort (CPUE) rates under population demographic uncertainty. Entries computed based on equations [D.3] – [D.5] for different combinations of age-1 and age-2+ COTS densities per hectare. Overall density is the summation of each age class' density. Jagged vertical line delineates the 3 COTS.ha^{-1} fertilisation threshold with orange shading denoting demographic uncertainty around CPUE = 0.03 COTS.min^{-1} for equilibrium CPUE corresponding to fertilisation threshold. Employed detection rates were α = 0.82 (age-2+) and β = 0.19 (age-1). In the absence of handling constraints, total diver detections (all potentially detectable COTS identified) of density may be estimated by multiplying α and β with their respective actual density per ha. Double line approximates the number of age-1 COTS to sustain an age-2+ population of given density (equilibrium calculations with M=2.56)—below the line suggests age-2+ growth and above the line suggests insufficient numbers to sustain age-2+ density (both based on mortality rates). Similar dynamics are indicated by the dashed line with M=1.76 (M sensitivity of Plagányi et al. 2020).

	CPUE	**Age-2+ detectable @ α (actual density)**												
		0.00 (0)	**0.82 (1)**	**1.64 (2)**	**2.46 (3)**	**3.28 (4)**	**4.10 (5)**	**4.92 (6)**	**5.74 (7)**	**6.56 (8)**	**7.38 (9)**	**8.20 (10)**	**12.3 (15)**	**16.4 (20)**
Age-1 detectable @ β (actual density)	**0.00 (0)**	0	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.04
	0.95 (5)	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.04	0.04
	1.90 (10)	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.04	0.04
	2.85 (15)	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.04	0.04
	3.8 (20)	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.05
	4.75 (25)	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.05
	5.70 (30)	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.05
	6.65 (35)	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.05
	7.60 (40)	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.05
	8.55 (45)	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	9.50 (50)	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	11.4 (60)	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	13.30 (70)	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.06
	15.20 (80)	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.06
	17.10 (90)	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06
	19.00 (100)	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06

Table 4. Expected catch-per-unit-effort (CPUE) rates under population demographic uncertainty. Entries computed based on equations [D.3] – [D.5] for different combinations of age-1 and age-2+ COTS densities per hectare. Overall density is the summation of each age class' density. Jagged vertical line delineates the 3 COTS.ha^{-1} fertilisation threshold with orange shading denoting demographic uncertainty around CPUE = 0.03 COTS.min^{-1} for equilibrium CPUE corresponding to fertilisation threshold. Employed detection rates were α = 0.82 (age-2+) and β = 0.34 (age-1). In the absence of handling constraints, total diver detections (all potentially detectable COTS identified) of density may be estimated by multiplying α and β with their respective actual density per ha. Double line approximates the number of age-1 COTS to sustain an age-2+ population of given density (equilibrium calculations with M=2.56)—below the line suggests age-2+ growth and above the line suggests insufficient numbers to sustain age-2+ density (both based on mortality rates). Similar dynamics are indicated by the dashed line with M=1.76 (M sensitivity of Plagányi et al. 2020).

	CPUE	**Age-2+ detectable @ α (actual density)**												
		0.00 (0)	**0.82 (1)**	**1.64 (2)**	**2.46 (3)**	**3.28 (4)**	**4.10 (5)**	**4.92 (6)**	**5.74 (7)**	**6.56 (8)**	**7.38 (9)**	**8.20 (10)**	**12.3 (15)**	**16.4 (20)**
Age-1 detectable @ β (actual density)	**0.00 (0)**	0	0.01	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.04
	1.70 (5)	0.01	0.01	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.04	0.04
	3.40 (10)	0.02	0.02	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04
	5.10 (15)	0.02	0.02	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.05
	6.80 (20)	0.02	0.03	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.05
	8.50 (25)	0.03	0.03	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	10.20 (30)	0.03	0.03	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	11.90 (35)	0.03	0.03	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05
	13.60 (40)	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.06
	15.30 (45)	0.04	0.04	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.06
	17.00 (50)	0.04	0.04	0.04	0.04	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06
	20.4 (60)	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06
	23.80 (70)	0.05	0.05	0.05	0.05	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.07
	27.20 (80)	0.05	0.05	0.05	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07
	30.60 (90)	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07
	34.00 (100)	0.06	0.06	0.06	0.06	0.06	0.06	0.06	0.07	0.07	0.07	0.07	0.07	0.07

3.2 Model fits in expanded CCIP MICE

It was not possible to fit all reefs and sites as initially intended (see section 2.3.4). This was because we needed to increase the number of control voyage visits from 6 to 12 to ensure sufficient data was available for each reef included in the modelling. The final reef list included 30 sites across 8 reefs. Preliminary attempts to fit the model with at least six control voyages did not allow for model convergence or resulted in a non-positive Hessian matrix which indicated that a solution was not stable (i.e. large parameter changes with fine scale changes, or with no changes, to initial parameter values). Model convergence was achieved when the minimum number of control voyages was increased to 12. The solution was stable and did not vary appreciably with model jittering. Reefs that we successfully fitted are listed in **Table 5** and shown in **Figure 4**. Model parameter estimates are provided in Appendix H. Example model plots are provided in **Figure 9**.

Table 5. Revised list of reefs to which the model was successfully fitted.

Assigned reef number	Reef ID	Assigned site numbers	Reef name	Latitude	Longitude
1	17-063a	1–2	Farquharson Reef	17.8099	146.495
2	18-027	3–7	Trunk Reef	-18.3349	146.784
3	18-043	8–9	Fore And Aft Reef	-18.5271	147.021
4	18-075	10–13	John Brewer Reef	-18.6416	147.035
5	18-079	14–16	Keeper Reef	-18.7454	147.281
6	23-077	17–23	Fitzroy Reef	-23.6393	152.141
7	23-082a	24–28	Lady Musgrave Reef	-23.893	152.424
8	24-008	29–30	Lady Elliot Island Reef	-24.1155	152.709

Alternative COTS feeding rate formulations were also considered. Namely this included allowing the feeding rate to either (1) be specified as a single term common to all reefs, (2) to vary by reef where each reef was fitted with an individual interaction term, or (3) to vary latitudinally such that all reefs at a given latitude (to the nearest degree) were fitted with an aggregate term. A model selection criterion, Akaike Information Criteria (AIC), was used to select the most parsimonious feeding rate formulation based on how many parameters were included and how well the resulting model fitted the data. The preferred model based on AIC was for a single feeding rate term common to all reefs (**Table 6**).

Table 6. Comparison of models with different feeding rate formulations. Model 1 employed a single feeding rate common to all reefs, Model 2 employed feeding rates specific to each reef, and Model 3 employed a feeding rate common to all reefs at a given latitude (to the nearest degree). Akaike Information Criteria (AIC) was used to select the most parsimonious model (lowest score) and is denoted in bold. Asterisk (*) denotes models that did not converge. Model 1 was most parsimonious (bold).

	Model 1	Model 2	Model 3
Likelihood value	6891.503	6758.877	6824.908*
Number of parameters	63	70	66
AIC	**108.3239**	122.3628	114.3433

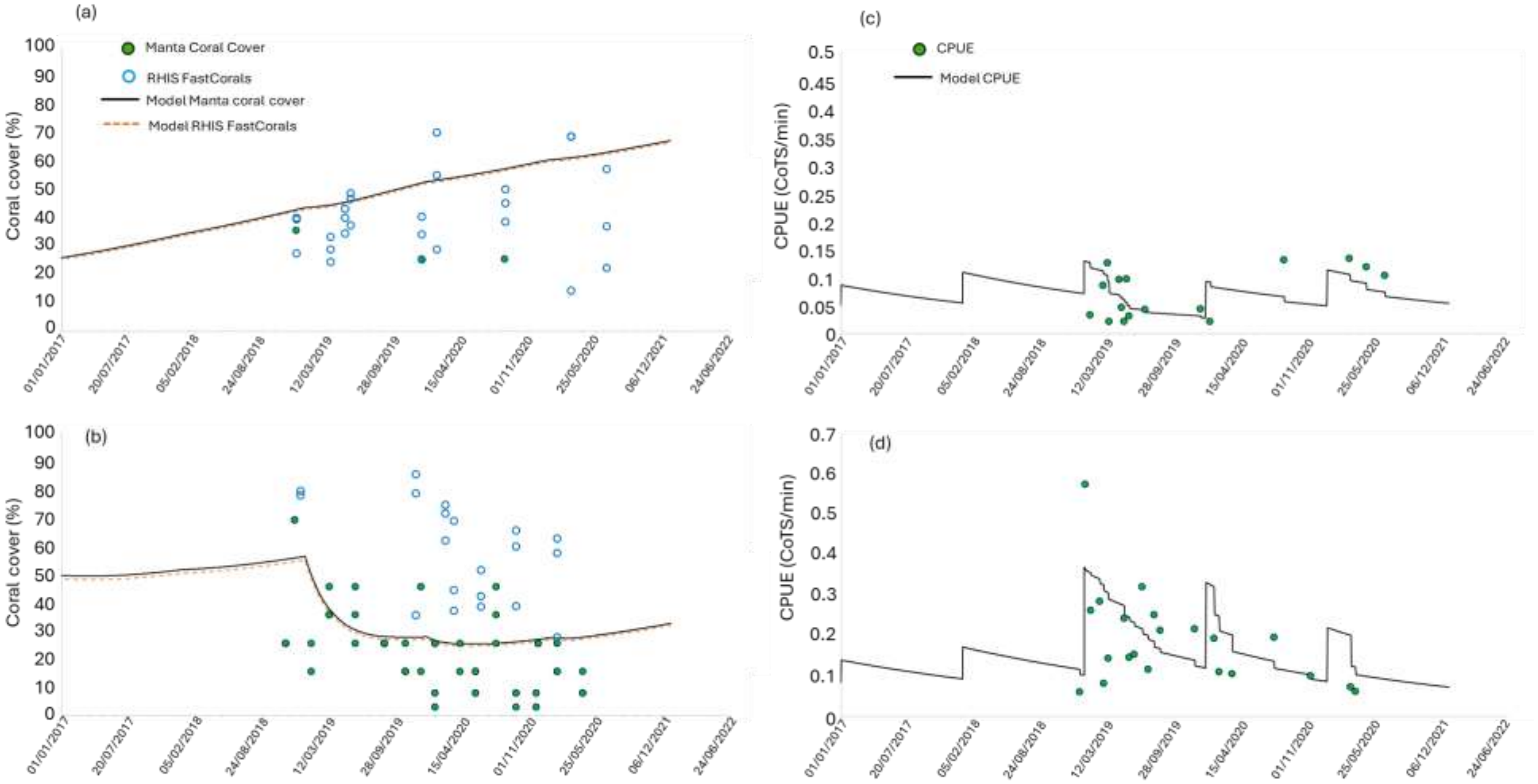


Figure 9. Example model fits for coral cover (%) at **(a)** Site 9 (Reef 3/Fore And Aft Reef) and **(b)** Site 10 (Reef 4/John Brewer Reef). Hollow blue circles are fast-growing coral observations from Reef Health Impact Surveys (RHIS) and solid green circles are total coral cover observations from the Crown-of-thorns starfish Control Program manta tows. The dashed orange line is the model-predicted coral trajectory of fast-growing corals and the solid black line is the model-predicted coral trajectory for total coral cover. Also shown are example model fits for crown-of-thorns starfish (COTS) Catch-Per-Unit-Effort (CPUE) rates (COTS.min^{-1}) at **(c)** Site 9 (Reef 3/Fore And Aft Reef) and **(d)** Site 10 (Reef 4/John Brewer Reef). Here, green solid circles are CPUE rates from the COTS Control Program and solid black line is the model-predicted CPUE trajectory.

3.3 Comparison of IPM and past or no intervention strategies

3.3.1 Comparison of IPM to past intervention (2013–2018)

Historical COTS control efforts from 2013 to 2018 largely focused on eradicating COTS from high value tourism sites. Since 2018, the COTS culling program has implemented control drawing on facets of IPM and no longer seeks to eliminate all COTS from selected reefs. The modern approach targets reducing COTS to "ecological management thresholds" (**Table 1**) such that corals can grow and recover (GBRMPA 2023), and it combines surveillance of reefs to detect when and where COTS are above threshold levels with a culling response. The way in which surveillance and culling are linked is referred to as the "simplified decision tree" (Fletcher et al. 2020). A representation of the simplified decision tree (**Figure 6**) was coded here and simulated across the time frame of 2013 to 2018 for comparison to the reef-level outcomes of the historical control program.

Both the mean and median are shown for the model suggested improvement in total coral cover (**Figure 10**) and for the model suggested improvement in coral cover relative to 2013 (**Figure 11**). The mean and median are both used to demonstrate that the coral cover outcomes derived from COTS control are likely to vary between different sites (and by extension, between different reefs). We only modelled a small set of locations so the mean is useful here as it reflects what COTS management could theoretically achieve. COTS control is suggested to be highly effective at some locations and more modest in other locations. This is evident in that the mean coral outcomes (both total and relative to 2013 – **Figure 10a** and **Figure 11a** respectively) are twice as high as the median coral outcomes (both total and relative to 2013 – **Figure 10b** and **Figure 11b**). The median lying lower than the mean suggests a left skew indicating a few locations derive a large benefit, but the distribution has a tail towards 0. The median is useful because it is more robust than the mean when data are skewed. The impact of the 2016 and 2017 bleaching events on corals varied across the GBR. Some areas saw larger coral cover losses than others. This can have a substantial impact on the short-term improvements in coral cover that come from managing COTS at a site (Rogers and Plagányi 2022). The median is better able to depict the risk posed by short perturbations (that lead to large levels of coral mortality e.g. severe bleaching) to the gains made by the Control Program. Bleaching events, such as the 2016 event which had a patchy and uneven signal in the sites modelled here, can cause stronger skewing of the data which the median reflects better. The greater consistency of the 2017 bleaching event saw most sites impacted and so it was detected by the mean as well. Therefore, both the mean and median are provided. **Figure 10** and **Figure 11** have been standardised to the number of hours divers spent underwater controlling COTS to compare the 'return on investment' of each dive hour used. The metric for the investment return is either total coral cover (**Figure 10**) or improved coral cover relative to 2013 (**Figure 11**). The historical intervention approach used a total of 2,796 hours to control COTS at the modelled sites from 2013 to 2018. Simulation of the current decision tree approach used a total of 1,892 hours, equating to 48 % less time than the historical control program. In doing so, the decision tree approach derived greater benefit (in terms of coral cover) from each dive hour invested.

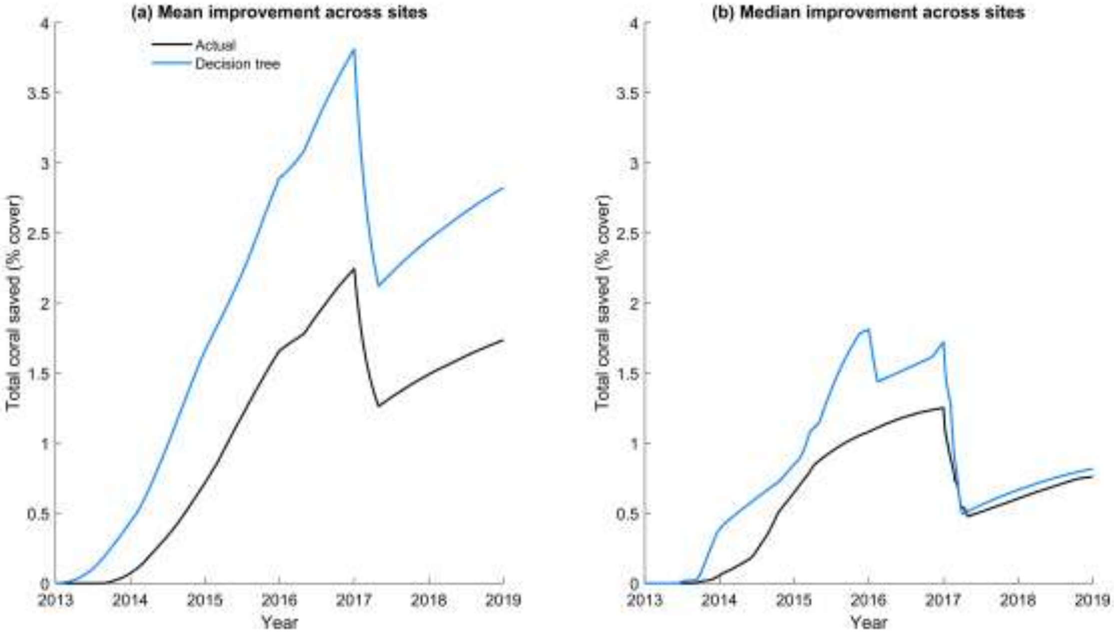


Figure 10. Model suggested improvement in total site coral cover over years 2013 to 2018 under either the implemented control ("Actual") over the time period, or under the simulated simplified decision tree ("Decision tree"). The differences are obtained by considering the difference between the Actual and Decision tree scenarios and a scenario of no control. Plots indicate the site level outcomes and do not reflect the potential benefits that saved (or lost) corals may have on regional coral cover through increased larval supply. Each scenario, Actual and Decision tree, used a different number of dive hours (2,796 hrs and 1,892 hrs respectively) to achieve their outcomes. Outcomes were standardised to the Decision tree scenario dive hours. Figure panels are **(a)** the mean improvement across the 13 sites, and **(b)** the median improvement across the 13 sites.

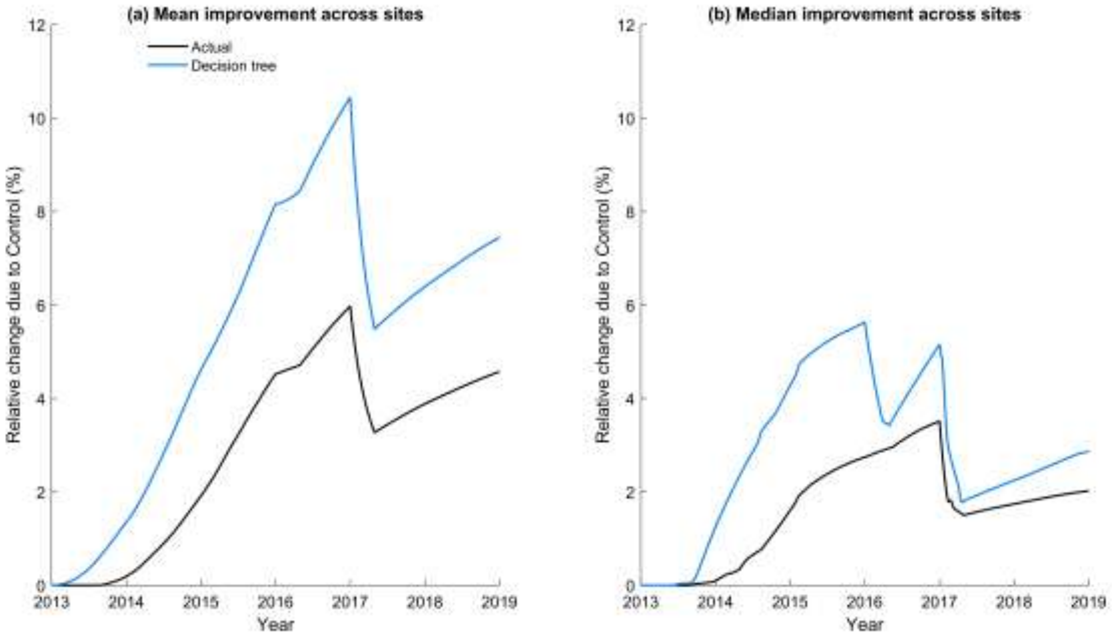


Figure 11. Model suggested improvement in total site coral cover over years 2013 to 2018 relative to 2013 under either the implemented control (“Actual”) over the time period, or under the simulated simplified decision tree (“Decision tree”). The differences are obtained by considering the difference between the Actual and Decision tree scenarios and a scenario of no control. The difference is considered relative to the initial coral cover in 2013 at the site. Plots indicate the site level outcomes and do not reflect the potential benefits that saved (or lost) corals may have on regional coral cover through increased larval supply. Each scenario, Actual and Decision tree, used a different number of dive hours (2,796 hrs and 1,892 hrs respectively) to achieve their outcomes. Outcomes were standardised to the Decision tree scenario dive hours. Figure panels are **(a)** the mean relative improvement across the 13 sites, and **(b)** the median relative improvement across the 13 sites.

3.3.2 Comparison of IPM to no intervention (2018–2021)

Using the expanded CCIP MICE (section 3.2), the efficacy of the COTS Control Program to improve coral cover at the site level was examined compared to a scenario where there was no COTS control. The fitted model was used to create a model-based counterfactual to the fitted trajectories by setting the time spent culling COTS at each site to 0 between years 2018 and 2021 (**Figure 12**). Comparing the fitted and counterfactual trajectories suggests that the mean amount of coral cover across the 30 sites would have been 8.0 % (median 7.2 %) higher than if COTS control was not implemented over the four-year period. Coral saved from COTS predation at the site scale may play an important role in the regional supply of coral larvae and broader scale coral dynamics. There was an increasing trend in the level of coral improved through COTS control such that each subsequent year of control saw increased total coral cover (mean and median) compared to if there was no COTS control.

Taken together, these two modelling scenarios conducted over different time periods and fit to data from different reefs and sites both suggest that the implementation of IPM principles (Fletcher et al. 2020) including the implementation of ecological management thresholds, has substantially improved the amount of coral cover that can be protected by the current

COTS Control Program compared to historical approaches (**Figure 10** and **Figure 11**) or no control (**Figure 12**).

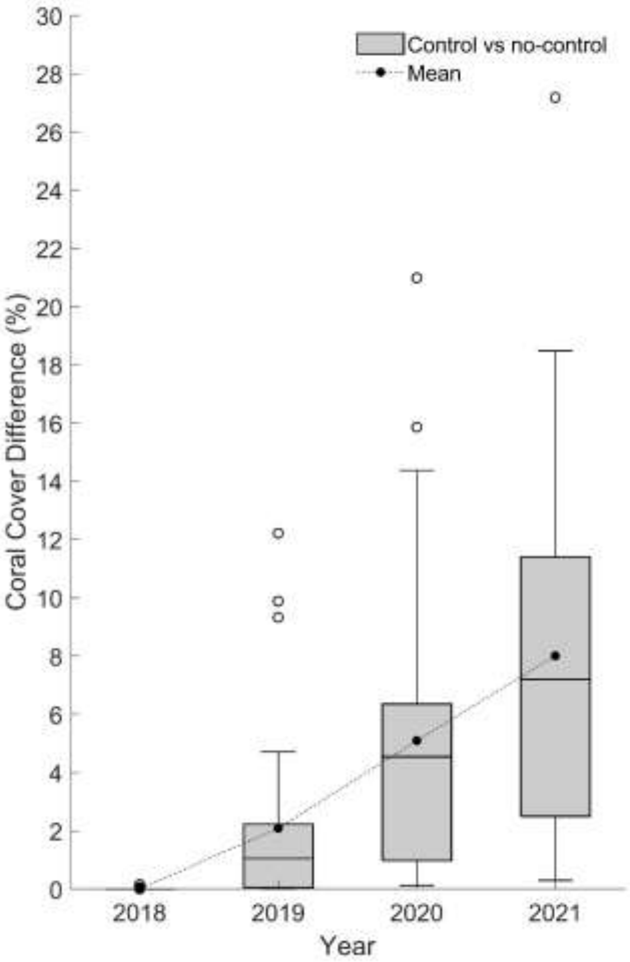


Figure 12. Modelled impact of COTS control on total coral cover over 2018 to 2021 at the site level. Difference in total coral cover is obtained from comparison of the fitted model trajectories with COTS control to a modelled counterfactual without COTS control (n=30 sites). Box and whiskers depict the mean coral cover difference (solid filled circle with dashed black line), median coral cover difference (middle line), the 25th and 75th percentiles (the box), and any outliers (hollow circles).

3.4 Fish as COTS predators framework development

A Schaefer surplus production model was fitted for red-throat emperor to standardised abundance indices and the model was forced with its estimated catch history for the GBR (**Figure 13**). The surplus production model is not a stock assessment and is a simple representation to capture dynamics of a generalised fish predator within an ecosystem model focused on coral and COTS. Data are available through recent assessment of the red-throat emperor stock at the GBR scale (Northrop and Campbell 2020) and so the carrying capacity (parameter *K* which is spatial scale dependent) was fixed and the intrinsic growth rate (parameter *r*) estimated. It was possible to estimate the intrinsic growth rate at a range of carrying capacity values however the reliability of the parameter estimate decreased as the fixed carrying capacity was increased (e.g. **Table 7**). This was due to the catch history not forcing the biomass dynamics to track sufficiently across the surplus production and biomass recovery curves given the contrast in the data (**Figure 14**) and the model fit of the intrinsic growth rate thus deteriorated. Model estimates of the growth rate are similar to those predicted from worldwide analysis of red-throat emperor (r=0.298; Thorson et al. 2023) and similar to what was assumed in historical GBR modelling of red-throat emperor (r=0.30; Leigh et al. 2006). The intrinsic growth rate for the base case (K=12,000 t) is used to capture fish dynamics for a generalised fish predator assumed indicative of identified COTS predators (e.g. red-throat and spangled emperor; Kroon et al. 2020; Kroon et al. 2021). The Schaefer surplus production model is implemented relative to carrying capacity in simulations to decouple the spatial dependence (introduced by specification of *K*) for use at the reef-scale based on GBR-scale model fits.

Table 7. Parameter estimates for Schaefer surplus production model fitted to red-throat emperor data. Model fits based on Northrop and Campbell (2020). The charter abundance index has units of number of fish per operation day, and the commercial abundance index has units of biomass (kg) per operation day, and modelled relative biomass are fitted to these at an annual time step. Computed catchabilities (q; a scaling constant) for each standardised abundance index are provided.

Unfished biomass (*K*; tonnes)	Intrinsic growth rate (*r*)	Standard deviation	Charter q	Commercial q
11,000	0.30	0.02	0.0105	0.0087
12,000	0.26	0.03	0.0087	0.0072
13,000	0.23	0.04	0.0073	0.0061

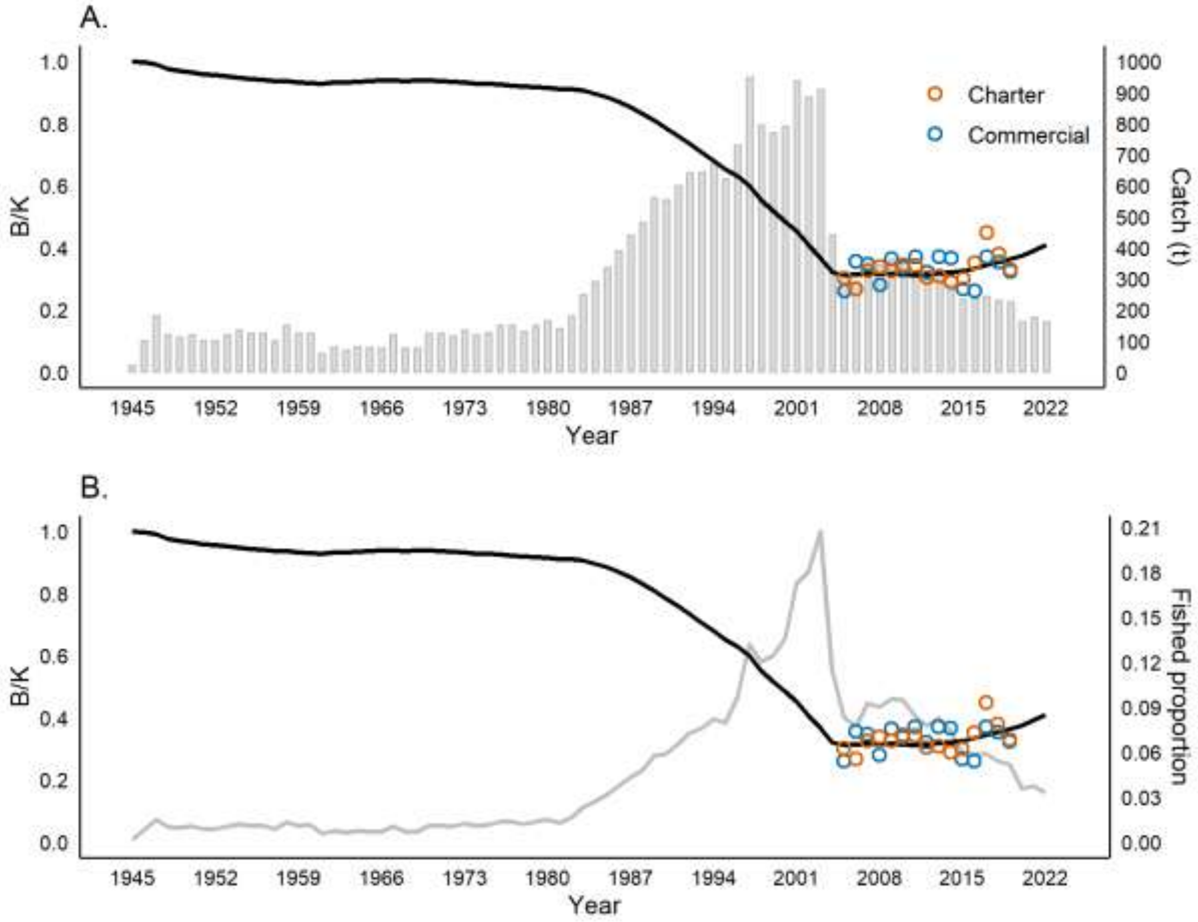


Figure 13. Model trajectories for red-throat emperor (*Lethrinus miniatus*) exploitable biomass depletion (black curve; fraction of unfished biomass *K*=12,000) and standardised catch-per-unit-effort data for charter (orange hollow circles) and commercial (blue hollow circles) operations (Northrop and Campbell 2020) are plotted on lefthand axis. **(A)** Annual total harvest (tonnes; grey bars), and **(B)** fished proportion of the modelled population are plotted on the righthand axis.

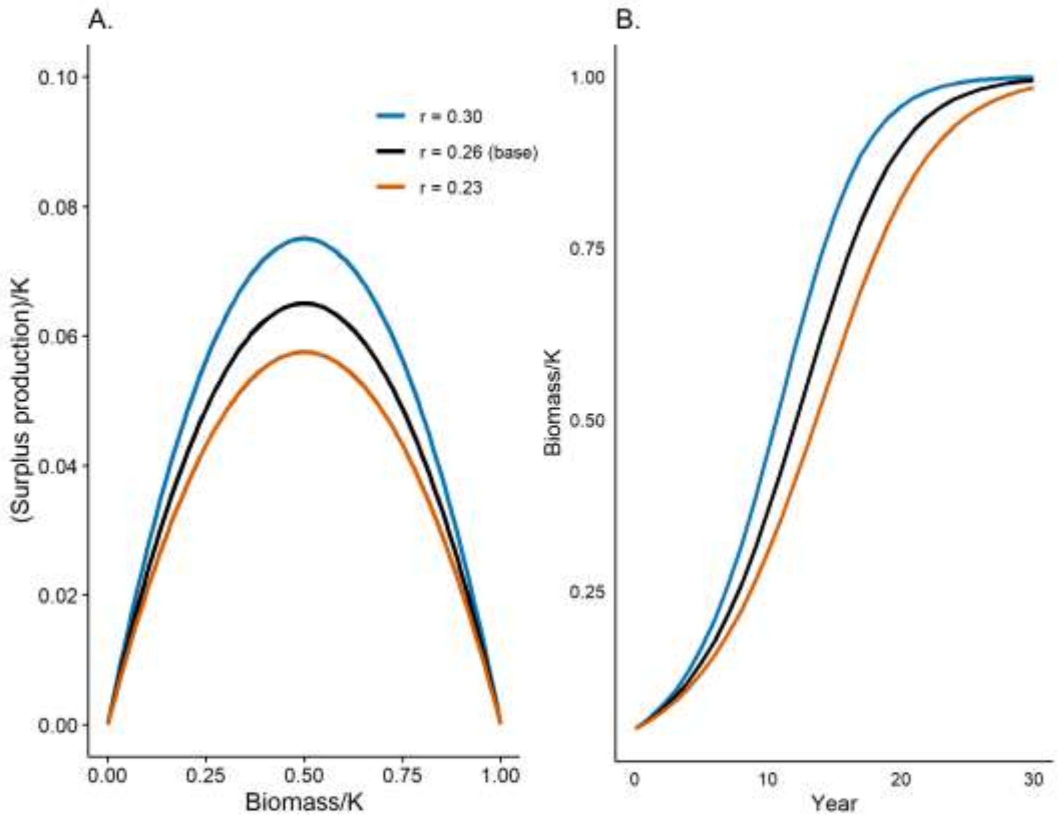


Figure 14. Surplus production curves arising from fitting a Schaefer production model to standardised abundance indices for red-throat emperor on the GBR. Curves are standardised to unfished biomass so that they can be generalised for spangled emperor. **(A)** Production as a fraction of unfished biomass achieved at a given stock depletion level, and **(B)** recovery trajectory from a depletion level of 5 % over 30 years.

4. DISCUSSION AND OUTPUTS

The present project (CCIP-R-03) was part of the Response subprogram and modelled coral-COTS dynamics at the reef scale with the aim of refining COTS control thresholds and evaluating COTS control performance. Specifically, we sought to develop and model how current COTS control thresholds are used, evaluate how effective the current approach to COTS control is relative to what has been done historically in terms of control efforts and in the absence of any COTS management. We also sought to provide a framework for how predators and COTS behavioural responses to predators can be included in GBR COTS models. Addressing these specific aims enables us to provide advice on which COTS management thresholds are relevant for different management objectives and when they are likely attainable, contribute to the building body of research that supports implementing COTS control as a recommended management action relative to doing nothing, identify the risk of environmental perturbations to COTS control outcomes dependent on how culling resources are used, and provide a framework to support future modelling of alternative COTS control options (fish as predators and COTS behaviour). This project thus contributes to the development of targeted decision support tools, allowing for more efficient and effective operational responses.

In this report, we expanded and applied a mathematical model (called a "Model of Intermediate Complexity for Ecosystem assessment" or MICE for short) that simulates coral, COTS, and manual COTS control. We drew on and extended previous MICE versions to investigate the generality of current COTS control thresholds (and considerations thereof), and the efficacy of the current IPM approach to COTS management (since 2018) compared to the historical (2013–2018) approach to culling. Importantly, we updated and validated our model using data from 2018 to 2021 from the COTS Control Program (cull data and manta tow data) and Reef Health Impact Surveys (for coral types at a location) so that it reflects observed trends in coral and COTS abundance and the effectiveness of the current Control Program. We also included reefs from different areas of the GBR so that the CCIP MICE can provide advice on reefs with different conditions. The updated model was used to infer the reef-scale benefit of COTS control since 2018 and provides a basis for future modelling of alternative management interventions and control (e.g. COTS predators).

Additionally, we synthesise (here and in appendix documents) the outcomes of Rogers et al. (2023). This publication benefitted from, and directly contributed to, the CCIP portfolio of work and discussions thereof and was summarised and communicated within CCIP. Rogers et al. (2023) developed and applied a reef-scale COTS-coral MICE to investigate the dynamic implementation of culling thresholds across a set of reefs (from which Effort Sink dynamics were identified and defined). The work featured heavily in CCIP, including a dedicated workshop session drawing on Rogers et al. (2023) and operationalising its concepts in CCIP regional modelling projects, and the provision of management advice for thresholds and reef selection (Appendix I: Communication Pieces). As such we include their management implications here (Section 4.1).

4.1 Integrated Pest Management and Effort Sinks (Rogers et al. 2023)

IPM aims to avoid economic and/or ecological losses by using our understanding of how a pest species interacts with it ecosystem to help define management thresholds where they can have a negative impact (Westcott et al. 2016; Stenberg 2017; Dara 2019). IPM has primarily been applied in terrestrial settings (e.g. agriculture) and the COTS IPM program is a rare example of IPM applied to a marine ecosystem. IPM relies on being able to detect (or predict) pest population dynamics, act on potentially harmful processes and trajectories, and having the management resources to facilitate meaningful control (Mouden et al. 2017; Dara 2019; Showler et al. 2021). There has, however, been limited quantitative analysis of how to optimise the use of such thresholds in the management of COTS. The scenarios examined varied in terms of their ecological threshold target, the sensitivity of the threshold, and level of management resourcing. The work suggests that within the context of management resource constraints, it is ideal to have approaches that allocate resources based on the latest information, and ecological thresholds. Moreover, the study found strategies that were not based on adjusting target CPUEs for coral cover and sustainable COTS densities (i.e. adaptive and ecologically based), may have had the potential to achieve similar (sometimes better) outcomes. However, the result depends on how diluted they are among sites and the operation of Effort Sinks. Over large areas and regions, the cost may be prohibitive to implement non-adaptive, or non-ecologically based, approaches.

The utility of thresholds for IPM lies in their ability to quantify progress and prioritise efforts and control strategies (Treska et al. 2021). However, whilst such thresholds quantify a level of suppression of a pest species at a location (Green and Grosholz 2021), the study showed through modelling that such thresholds can cause Effort Sink dynamics when also considering where and how to use thresholds. An Effort Sink is fundamentally a function of resource constraints (implicitly, spatial dilution), management targets, and the ecological dynamics in question. Effort Sinks are not just a function of the ecological dynamics nor the management dynamics; they are an emergent property of the integrated dynamics. Effort Sinks can emerge when there is a mismatch between the metrics used to assess performance, resources available to support management, and the spatial scale at which management is assessed.

Specific to COTS management, Effort Sinks can be defined as a reef (or even site) that uses up lots of control time that cannot then be used at other reefs and detrimentally impacts the coral outcomes across the set of locations prioritised for COTS control. High COTS recruitment and low threshold targets (e.g. Allee-based threshold under outbreak conditions) created strong Effort Sinks. Controlling to threshold level(s) can necessitate repeated prioritisation of a reef before other reefs are visited (Fletcher et al. 2020). However, COTS culling efforts become increasingly more costly as catch-rates decrease, due to limited detectability and cryptic emergence rates (Fletcher et al. 2020; Plagányi et al. 2020; Westcott et al. 2020). Established COTS outbreaks on the GBR substantially exceed current resourcing capabilities and as such effort must be prioritised (Fletcher et al. 2020).

In simulations, if resourcing was inadequate and the target thresholds were low (e.g. 0.03 COTS.min^{-1}), and particularly if there was high COTS recruitment to a site, then much of the available management effort could be spent at only a few sites to attain ecologically meaningful results. Strong sinks, and having sufficient resources, could be particularly important where the main beneficiary of management efforts (faster growing coral here) are also highly susceptible to other perturbations (e.g. coral bleaching; Marshall and Baird 2000; van der Zande et al. 2020) as derived management benefits may be disproportionally impacted if they are too spatially concentrated.

Limitations of the study included modelling few reefs with high coral cover, and that logistical (travel) and metapopulation dynamics were not modelled. Differences due to COTS control may have been larger under lower levels of coral cover (but see Rogers and Plagányi 2022) and the importance of a given change for reef condition is likely to also depend on interpretation alongside other indicators (e.g. Mumby et al. 2014; Hein et al. 2017). Some spatial factors were not modelled. These were boat travel considerations (e.g. travel time), that inter-reef larval exchange was implicitly captured, and that we assumed omnipotent surveillance for threshold-based scenarios (cf. Type I and Type II errors; Westcott et al. 2021a). Integrating with a regional model (e.g. Condie et al. 2021) that resolves reef locations and processes was suggested as a way to provide insight into how aligning reefs and reef management sites impact the performance of different control scenarios.

4.2 Generality of culling thresholds

Our analysis suggests that under conditions of reduced coral growth capacity, such as following bleaching events (Pratchett et al. 2009; Hughes et al. 2019b) or more generally at higher latitudes (e.g. Anderson et al. 2017), the expected benefit to coral cover by varying COTS management thresholds was limited compared to if coral growth was unaffected. Practically, in locations that have lower coral growth capacities, controlling to substantially below the equilibrium threshold may have limited immediate benefit to coral cover at the control location. This does not consider the potential regional level benefits, such as COTS reproduction ramifications that are more favourable for coral management when COTS densities are maintained at very low densities (Hock et al. 2014; Hock et al. 2017; Rogers et al. 2017). CPUE targets based on coral growth and COTS catches are likely to be robust to differences in coral growth rates but the subtle difference between preventing coral cover decline and improving coral cover requires local contextualisation. The MICE indicates that the consequences of not achieving equilibrium thresholds remain similar, but the benefits of surpassing equilibrium points may reduce depending on coral cover and growth potential.

COTS at high densities (outbreaks) can consume corals much faster than the corals can grow which can lead to coral declines (e.g. Pratchett et al. 2009; Kayal et al. 2012). Our work indicates that avoiding coral loss (as opposed to recovery) is the most amenable and currently tangible objective of COTS control. We found that culling to lower than 0.04 COTS.min^{-1} is unlikely to substantially improve coral trajectories at the site of control unless coral growth is much faster than currently assumed. Targeting CPUEs <0.04 COTS.min^{-1} may also lead to “Effort Sinks” (Rogers et al. 2023) whereby a few sites take longer to control which, given finite resources, limits the potential to control other sites. Unless the goal is to suppress COTS reproduction (the Allee threshold), it may be unnecessary to persist to <0.04 COTS.min^{-1} to limit coral loss. As COTS preferentially consume faster growing corals (Pratchett 2007), maintaining their densities around equilibrium levels (0.04–0.08 COTS.min^{-1}) could still allow for corals to recover at controlled sites as COTS decline (e.g. through predation; Kroon et al. 2021; Desbiens et al. 2023). The applicability of <0.04 COTS.min^{-1} thresholds may include before an outbreak becomes widespread (Babcock et al. 2020), or in places where coral is very low and restoration activities are taking place (Ladd and Shantz 2020).

At low coral abundance COTS predation is likely to intensify on remaining corals and have a larger impact on coral dynamics (Haywood et al. 2019; Keesing et al. 2019). Consequently, the sustainable number of COTS on a reef is likely to be low irrespective of coral growth rates. Low coral abundance limits the difference in the supported COTS density for different coral growth rates because there is less coral to be potentially lost and less to potentially proliferate. At high coral cover, the main cause underpinning modelled differences in coral cover loss among scenarios is COTS predation effects. Removing COTS from sites with >20 % coral cover is likely to have a larger impact on coral dynamics as predation effects are effectively saturated relative to available coral when coral cover is low. This means that many more COTS may be supported but that differences in coral growth rates will have a larger impact on how many can be sustained. At higher coral cover (~40 % to 80 %), the consequences of reduced growth capacity are amplified, based on the Schaefer model assumption that at these levels, corals are near their maximal growth rates given density-dependent effects. This contributes to the differences in the number of COTS that could be supported before coral cover declines.

COTS feeding preferences for corals with compromised health (e.g. bleached) are not known. It is likely that as preferred prey abundance decreases (e.g. bleached or died) then COTS will switch to eating less preferred corals (Pratchett 2007) and this response was captured at different fixed levels of preferred prey depletion. We did not model factors that could impact coral health, only differences in coral growth rates, and this implicitly assumes that COTS only consider live or dead coral and not the health of a coral. If COTS respond to coral health status, then our results can be generalised by considering COTS avoidance of a health condition as “dead” coral and therefore reduce the live coral cover accordingly (e.g. if COTS show a preference for a healthy non-preferred coral over a bleached preferred coral). Notably, studies from reefs in the offshore Pilbara region (Western Australia) observed the persistence of COTS selectivity for fast-growing over slower-growing corals in the aftermath of a mass bleaching event (Haywood et al. 2019; Keesing et al. 2019).

Cumulatively, the similarity of equilibria across different coral growth rates suggests that coral loss due to COTS is similar irrespective of growth capacity, but that recovery is likely to be heterogenous and dependent on the local prevalence and demographics of corals within management sites. This indicates that preventing coral cover loss versus improving coral cover through manual control are mostly separate objectives with limited overlap in terms of the required level of resourcing (i.e. they are most aligned for 25 % to 40 % coral cover with diminishing returns for sub-equilibrium targets elsewhere). Recently, typical coral cover has been reported at a region-wide mean of 35.7 %, 30.8 %, and 33.8 % in the Northern, Central, and Southern GBR regions respectively (Australian Institute of Marine Science 2023). For on-water control, this suggests that reefs, with typical coral cover, are likely to see both mitigation and bolstering effects of COTS control on corals under current culling thresholds. The general applicability of current thresholds is also likely to reduce additional costs that may be associated with resolving reef-specific thresholds (e.g. greater surveillance) and the complexity of threshold implementation.

4.3 COTS demographic uncertainty and culling thresholds

If density-based thresholds are to be targeted with CPUE then precautionary targets should be used to reduce the degree to which uncertainty may compromise the desired impact(s) of management (e.g. suppression of reproductive potential). As an example, we use the reproductive threshold of 3 COTS.ha^{-1} (Rogers et al. 2017) which may be applicable to limit COTS spread from reef to reef between outbreaks (see Rogers et al. 2023). Noting that detectability varies by age-size, the CPUE corresponding to an age-2+ density of 3

COTS.ha^{-1} is ~ 0.03 COTS.min^{-1} based on equilibrium dynamics and COTS becoming reproductively mature from 2 years of age (computed here and as per age-2+ COTS.ha^{-1} for SCUBA based CPUE, Table 3.1; Plagányi et al. 2020). However, at least initially, a CPUE representation of the density threshold may need to be more conservative to reflect uncertainty around the age composition of the population being controlled. Our model accounts for the fact that smaller COTS are often not culled and that under dynamic conditions these individuals may mature and reproduce during the next summer season. Because the relationship between CPUE and COTS density is not linear, and because COTS detectability changes across ages (sizes), the same COTS population density but with different demographics can lead to different CPUE values. For the reproductive threshold, a precautionary CPUE of ~0.01–0.02 COTS.min^{-1} may be more appropriate (at first) than the analytical value of 0.03 COTS.min^{-1} that was calculated under equilibrium dynamics. As certainty around the size composition of COTS at a location increases (e.g. demographic information from number and age of culled COTS), stringent CPUE thresholds could be relaxed accordingly. A focus on just CPUE may result in bias towards locations with COTS of higher detectability (age-2+ COTS here) such that age-1 skewed populations of potentially similar or higher densities receive less focus. In practice this could lead to largely reduced CPUEs with a less substantial impact on underlying densities (i.e. including age-1 COTS) which aligns with conclusions between the pre-IPM and IPM Control Programs drawn by Westcott et al. (2021b). We also highlight for the purpose of this example, that if low CPUEs are targeted during COTS outbreaks (or more generally when resources are stretched), then Effort Sink dynamics may emerge. Our discussion relates to the potential applications of the reproductive threshold between outbreaks when it may be feasible.

4.4 Current versus historical COTS culling implementation

The COTS Control Program has undergone substantial changes over the past 10 years (Westcott et al. 2021b). One of the biggest changes is the introduction of the simplified decision tree in 2018 to assist in identifying where, and how, COTS control will be conducted (Fletcher et al. 2020). From 2013 to 2018, the COTS Control Program focused on controlling high COTS densities at sites on important reefs (e.g. high value tourism sites). In 2018 the program was revised to incorporate ideas from the agricultural concept of IPM. A key idea of IPM is to use a structured approach to manage a pest species (COTS) so that they have minimal impact on some asset of value (coral cover). As part of the IPM revolution, there was an important shift from culling as many COTS as possible at individual sites on a reef to controlling COTS around the entire reef and only culling enough to avoid coral cover loss. The way in which the IPM achieves this is through the simplified decision tree which is underpinned by scientific research which informs threshold values.

We simulated how the simplified decision tree might have protected coral cover compared to the previous approach from 2013 to 2018. We found the decision tree approach outperformed the historical approach and would have likely led to higher coral cover; especially if ‘saved’ time was able to be used at other reefs (i.e. controlling more reefs in the region). To achieve the same coral outcomes at the reef-scale as the historical approach, the decision tree approach required approximately 1,000 fewer dive hours. If these resources were reinvested into the same reefs, the mean amount of coral that could have been preserved between 2013 and 2018 was almost double that of the historical approach (up to approximately 70 % more coral preserved). It was also found that median coral cover was greater under the decision tree simulations compared to modelled actual scenario outcomes. The median outcomes were lower than the mean outcomes which suggests potential Effort Sink dynamics. The presence of Effort Sink dynamics indicates potential resource concentration and that invested efforts may be at higher risk of loss through perturbations (e.g. a bleaching or cyclone event).

Much of the short-term coral gains from COTS control are for faster growing corals (see also Condie et al. 2018). However, faster growing corals are also more susceptible to perturbation (e.g. bleaching mortality). As most of the short-term benefit from COTS control is mitigating damage to those faster growing corals, COTS control-mediated coral improvement could be drastically reduced if there is severe bleaching at a control reef ('higher risk'). For the set of reefs modelled, this may have occurred during the 2017 bleaching event. Focusing on reefs that are less likely to experience severe bleaching (and mortality) and/or those that are more robust to such events would likely reduce management risk (as defined above) and maximise the potential benefits derived from COTS control (Rogers and Plagányi 2022).

The decision tree guides the control of sites until all sites at a reef are below their CPUE threshold (Fletcher et al. 2020). If a site was intensively controlled and then bleached in the next one to two years, this would have a substantial impact on median coral improvements attributable to COTS control (Rogers and Plagányi 2022). The impact is because control efforts were concentrated which led to higher coral (which was also highly susceptible to bleaching induced mortality) and therefore the site had more coral to lose. As such, the decision tree approach may carry a higher risk to environmental perturbations during the early implementation due to spatial concentration of culling efforts. However, while bleaching at an intensively controlled site was a setback, the reduced number of COTS allowed the corals to recover more quickly under the decision tree scenario than the actual scenario. Overall, the ability of the decision tree scenario to improve coral cover and increase recovery speed following perturbation suggests that it is more beneficial to coral resilience at a site than the non-decision tree informed practices used in the past. Results provide model support that the decision tree has made a substantial improvement to the efficacy of COTS control in that each dive hour invested provides a greater return in coral cover.

Given the provision of recent data following implementation of the decision tree and IPM COTS culling program, the model was updated and fitted to data from 2018–2021. This allowed for a direct comparison between COTS control implemented under the decision tree approach and a model-based counterfactual of if no control was conducted. The model-based counterfactual for COTS control efforts over 2018–2021 indicated that the mean total coral cover was 8.0 % (median 7.2 %) higher than if control had not been conducted. Cumulatively, the increased efficacy of the decision tree compared to historical control approaches and its ability to promote higher coral cover than what would otherwise eventuate supports COTS control as an effective means to increase local coral cover. Increased local coral cover may promote higher regional cover (sensu Hock et al. 2017).

4.5 Project outputs

The final outputs of this project include:

- Expansion and validation of MICE model (fit to COTS and coral data from 2018–2021 across more reefs and sites).

- Validated efforts of the current Control Program by estimating potential coral cover benefit from COTS control vs a counterfactual no control for the current Control Program (2018–2021).
- Using a MICE, estimated the potential coral cover benefit that may have arisen from implementing the IPM decision tree over the historical approach from 2013–2018 (which included two bleaching events).
- Extended and published on work that assessed how the availability of COTS culling resources traded off with the dynamics of COTS and corals and CPUE targets used to guide culling (Effort Sinks).
- Made recommendations on adjustments to CPUE targets based on how coral growth and COTS demography influence culling targets. Made suggestions on when different target CPUEs may be relevant depending on manager objectives for a reef and/or stage in the COTS outbreak cycle (e.g. using a target threshold for coral protection or spawning disruption).
- Formulated a framework for MICE to assess the influence of fish predators and fishing pressure on COTS abundance, behaviour and management.
- Provided an information brochure synthesising how different CPUE targets (thresholds), Effort Sink dynamics, and choices to conduct COTS control on bleached reefs are related and considerations for management.

Table 8. Summary of publications that have benefited or arisen from CCIP-R-03 works and discussions mapped against (abridged) project aims. Green indicates findings delivered here and orange indicates works in progress made possible through the model development of CCIP-R-03.

Publication	**Funding**	**Aim**		
		Refine ecological thresholds considering local factors	*Evaluate relative performance of different intervention strategies and characterise efficacy of recent IPM-based COTS control*	*When/where different interventions are most effective*
Improving coral cover using an integrated pest management framework (**Rogers et al. 2023**)	CSIRO **CCIP** UQ	Low thresholds not recommended in outbreaks.	Ability to cull first priority then thresholds. Ecological management threshold/Effort Sinks.	Need high COTS recruitment AND coral to protect. Allee threshold (Rogers et al. 2017) may be ok between outbreaks.
Culling corallivores improves short-term coral recovery under bleaching scenarios (**Rogers & Plagányi 2022**)	CSIRO UQ			Bleaching can disproportionally impact COTS control outcomes. Intervention outcomes likely more robust in less thermally-sensitive areas.
Validating effectiveness of COTS control thresholds to limit coral loss throughout the Great Barrier Reef (**Rogers et al. 2024**)	CSIRO **CCIP**	Coral growth of limited impact if limiting coral loss focused, more important if recovery focused. Important for CPUE thresholds to monitor COTS demographics. May need 0.06 COTS.min^{-1} CPUE threshold at 40 % coral cover and 0.8 COTS.min^{-1} at 60 % cover.		Limiting coral loss may be best for 20–50 % coral cover, recovery similar at 25–55 %. Current thresholds fit-for-purpose for limiting coral loss (current goal) and potential benefit from slight adjustment at 40–60 % coral cover.
Evaluation of site-level COTS control: Past versus present performance	CSIRO **CCIP**	Dynamically evaluate different threshold(s) with current decision tree approach.	Current approach more effective than historical. Post-2018 has seen steady improvement	

Publication	**Funding**	**Aim**		
		Refine ecological thresholds considering local factors	*Evaluate relative performance of different intervention strategies and characterise efficacy of recent IPM-based COTS control*	*When/where different interventions are most effective*
(**Rogers et al. *in prep***)		🟧	in coral vs counterfactual.	
Incorporation of fish predators and COTS behaviour (**Rogers et al. planned**)	CSIRO **CCIP**		How do fish predators influence manual control.	How to synergistically leverage predators in COTS culling.

5. RESEARCH SYNERGIES AND NEXT STEPS

Below we describe research synergies between this project and other CCIP projects, summarise how the outputs from this project can be integrated into other research, and importantly how the outputs translate into benefits for the COTS Control Program. Finally, we conclude with next steps and priority research areas for the coral-COTS MICE in the future.

5.1 Synergies

5.1.1 Prediction subprogram

There were a number of synergies with projects in the Prediction subprogram including: CCIP-P-01: In-situ feeding rates of COTS (Pratchett et al. 2025a) and fate of prey coral; CCIP-P-05: Resolving the impact of benthic and cryptic predation on COTS (Wolfe et al. 2025) and CCIP-P-06: Quantifying predation rates on COTS relative to fisheries management zones and corresponding differences in abundance of putative predators (Doll et al. 2025). Given that the field-based projects and this project ran in parallel, it was not possible to incorporate any outputs from the Prediction subprogram into the MICE. However, going forward, data from CCIP-P-01 may help to provide an estimate on daily feeding rates across different densities of COTS. These estimates can then be incorporated into the MICE to help refine COTS predation rates on coral e.g. seasonal consumption rates. Data from CCIP-P-05 (Wolfe et al. 2025) will provide information on the identity of benthic predators on juvenile COTS and mortality rates of juveniles. This information can be used to develop a juvenile COTS sub-model or help inform mortality of juveniles in the current MICE. CCIP-P-06 (Doll et al. 2025) aimed to quantify rates of predation on COTS at reefs with contrasting predator densities, including abundance and composition of potential COTS predators. Information collected from this project was used to help inform the modelled predator component in the MICE and in future will help inform scenario testing relating to predator abundance e.g. green vs blue zones, and predation rates for direct consumption of COTS.

5.1.2 Detection subprogram

Projects from the Detection subprogram that will likely be of benefit to the coral-COTS MICE in the future include CCIP-D-02: Tool Comparison (Lawrence et al. 2025) and CCIP-D-04: The COTS Surveillance System (Bainbridge et al. 2025). In particular, CCIP-D-04 (Bainbridge et al. 2025) aimed to provide new COTS and coral monitoring technology allowing for automated and rapid detection of COTS and benthic habitats. This could allow more spatial coverage in the model including further data with which to fit the model. Moreover, the improved technology could assist in providing improved data availability and quality to be able to separate coral groups more finely in the MICE.

5.1.3 Response subprogram

The coral-COTS MICE relies heavily on data from the COTS Control Program on numbers of COTS removed, cull rates, and coral cover. The provision of these data in a structured and timely manner is critical for efficient model outputs. As such the CCIP-R-01 (Fletcher and Rezvani 2025) project on information infrastructure will provide underpinning support for the MICE going forward, for example, assisting with reliable and timely sharing of data.

Future work could also include the coupling of sub-reef models such as MICE to larger, regional models (e.g. CCIP-R-04, Skinner et al. 2025) or allow for comparisons between other models that include predators (e.g. CCIP-R-10, Ceccarelli et al. 2025) or use in a model ensemble.

5.1.4 Informing future research needs

In revising ecological thresholds and testing demographic uncertainty, our MICE highlighted the following priority areas, which could be explored through future research endeavours and links with other CCIP program areas:

- The importance of estimating remnant or cryptic COTS at a site and their population age-size composition because detection biases manifest in CPUE.
- Comparisons of COTS density among studies (or even dissimilar reefs) may also benefit from considering uncertainty potentially introduced by variable detectability, especially when it is related to current culling operations. This underscores the need for data to better calibrate and fit COTS-coral interactions ideally consistent with the structuring of data from control and monitoring programs.
- Understanding how COTS interact with corals under different conditions (e.g. different coral communities, COTS demography, climate and temperature impacts) would enable better estimates of how CPUE—a function of COTS density, demographic composition, and detection rates—may link to coral dynamics (the basis for current management targets). Such data may be used in a dynamic MICE.
- Catch age-size composition information and detectability estimates could help adaptively calibrate site-specific thresholds.

In exploring the efficacy of the IPM approach, our modelling efforts suggested more consideration is needed around (1) what constitutes “excessive” effort at a reef and when is it not worth attempting control, (2) how should “risk” be defined so that it is responsive to management objective(s), (3) what is an “acceptable” level of risk, and (4) how might risk interact with management priorities to define sets of priority reefs. Quantitatively exploring these questions with the use of further modelling simulations could help to provide an actionable basis for both strategic (e.g. defining priority reef lists) and tactical on-water management decisions (e.g. when it is not worth controlling a reef).

5.2 Next steps

Developing an expanded modelling framework that can assess the impacts of other system components (e.g. fish predators, climate) on COTS control was a key objective of this project and provides an important intermediary step to translate key empirical research into potential management options for improving the day-to-day operation of the COTS culling program. As the CCIP concludes and the findings from empirical-based studies become available from other subprograms, these outputs can be used in the MICE.

The immediate next steps for this project are to work with other projects (e.g. CCIP-P-06, Doll et al. 2025 and CCIP-P-05, Wolfe et al. 2025) and obtain data on the interactions between COTS and key predators and how these interactions may vary (e.g. across levels of fishing pressure). Using these data in the MICE will then allow us to evaluate alternative fishing and COTS behavioural response scenarios. For example, if COTS respond to increased predation pressure via increased cryptic behaviour, then how is a reef's protection status (with regards to fishing) likely to influence culling investment at the reef. Alternatively, under increased fishing pressure, are COTS likely to deplete local corals faster and require rapid culling effort to limit their impact versus a reef of comparable COTS status but where fish presence reduces the rate of coral decline. This work is expected to be completed by the end of 2024 and shared via a journal article.

There are of course several future research directions and below we list the top priority areas for further research and development relating to the use of MICE on the GBR:

- Integrating information from field-based studies on COTS predation (juvenile COTS predators (CCIP-P-05, Wolfe et al. 2025) and adult COTS predators (CCIP-P-06, Doll et al. 2025) into the MICE.
- Further application of a climate change lens on the MICE modelling, for example, to better understand how COTS (as opposed to only coral) will respond to marine heat waves (e.g. impacts on COTS survival, growth, reproduction) and how this might impact COTS control (e.g. management thresholds, reef revisitation frequency, reef prioritisation). Also, further consideration of different coral groups (with different thermal tolerances) in the model, particularly under climate change, could help capture the range of potential coral and COTS responses and inform refined management action(s).
- Integrate new monitoring technologies (e.g. CCIP-D-04, Bainbridge et al. 2025), and SALAD surveys into the MICE framework to help inform model.
- Integrate both monitoring and understanding of coral-COTS-climate dynamics from the Torres Strait with the rest of the GBR to help understand the source of outbreaks, and how transferable guidance around optimal culling thresholds for COTS management in the GBR is to the Torres Strait.
- Application of MICE as an operating model in Management Strategy Evaluation (MSE) to transparently and quantitatively evaluate the trade-offs of different COTS control strategies and associated uncertainties in achieving a range of management objectives.
- Potential for MICE to be expanded for use in the Reef Restoration and Adaptation Program (RRAP) with a focus on coral restoration and evaluate restoration strategies under climate and COTS threats.

6. MANAGEMENT IMPLICATIONS AND IMPACT

6.1.1 Refining ecological thresholds

Overall, we found that it is important to account for Effort Sinks in management approaches. Threshold-based methods with greater tolerance (higher CPUE catch rate targets) performed well under both outbreak and non-outbreak conditions as they better balanced effort in line with ecological priorities and resourcing constraints which are critical to the annual reef prioritisation process. Stringent strategies (low catch rate targets) were not feasible under outbreak conditions, though our results suggest that they would otherwise be attainable outside of outbreak periods for a handful of key priority reefs and their management sites. Consequently, optimising control protocols that span pre- and early-outbreak periods as well as outbreaks themselves (Babcock et al. 2020) could be most effectively achieved through using ecological thresholds, namely those based on coral cover. Targeting low catch rates, such as those needed when coral cover is very low or to attain the Allee threshold, is suggested to be most feasible during non-outbreak periods. Low targets would require greater resourcing than we considered here to be continued under outbreak conditions and operational capability would need to be maintained between outbreaks to manage population dynamics before they exceed management constraints.

We found strategies with low target density thresholds for COTS (≤0.03 COTS.min^{-1}) could act as Effort Sinks and limit the number of sites that could be effectively controlled, particularly under COTS population outbreaks. This was because a handful of sites took longer to control which meant other sites were not controlled. Higher density thresholds (e.g. 0.04–0.08 COTS.min^{-1}) tuned to levels of coral cover, diluted resources among sites but were more robust to resourcing constraints and pest population dynamics. Four related questions that arise from the Effort Sinks work include (1) what constitutes “excessive” effort at a reef and when is it not worth attempting control at a reef, (2) how should “risk” to environmental perturbation(s) be defined so that it is responsive to the management objective(s) for a reef and the spatial concentration of efforts, (3) what is an “acceptable” level of risk, and (4) how might risk interact with management priorities to define sets of priority reefs (Effort Sink dynamics may also be a function of the set of priority reefs to control as well as e.g. resource and ecological dynamics). Quantitatively exploring these questions with the use of further modelling simulations could help to provide an actionable basis for both strategic (e.g. defining annual priority reef lists) and tactical on-water operation decisions (e.g. when is it not worth controlling a reef?).

Given the limited extent of current COTS detectability estimates, and the feasibility (and specificity) of targeting low CPUE levels, the most pragmatic approach is likely to maintain current thresholds for protecting coral cover or to target a CPUE of ≤0.04 COTS.min^{-1} for the fertilisation threshold. Introducing a CPUE threshold of 0.06 COTS.min^{-1} for coral cover from 40 % to 60 % may limit potential coral cover losses near 40% where the current threshold graduates from 0.04 to 0.08 COTS.min^{-1} but this requires further modelling (sensu Rogers et al. 2023) to assess. A reduction from 0.04 to 0.02 COTS.min^{-1} amounts to <1 COTS on a 40-minute dive and redeploying divers to remove an additional COTS is unlikely to substantially improve coral cover at the site and could lead to Effort Sinks that compromise coral cover on other reefs (Rogers et al. 2023). Therefore, implementing such thresholds should be done judiciously to avoid over-investing effort to the detriment of other reefs. Selectively focusing on older cohorts of a population could be favourable if trying to suppress reproductive output from a location but may be misaligned if trying to avoid loss of coral at a specific location, or where pre-emptive culling is being conducted to prevent renewed population irruptions (e.g. Chandler et al. 2023).

Our work indicated that coral growth would need to be substantially higher (65 %) than our base case to be comparable to the Keesing and Lucas (1992) threshold based on extrapolating in situ feeding rates of COTS at Davies and Little Broadhurst Reefs (south of Lizard Island). Their work suggests strong temperature dependent effects on COTS feeding rates (via seasonal effects), with summer feeding rates being roughly twice that of winter rates (Keesing and Lucas 1992). Both Davies and Little Broadhurst are much further south than Lizard Island and temperature dependence in COTS feeding rates may explain the difference between studies. Given published seasonal and latitudinal differences and patterns in coral growth rates (Anderson et al. 2017; Anderson-King et al. 2023), it is tenuous that coral growth differences completely account for the discrepancy. The Keesing and Lucas (1992) threshold may be higher than we found because they assume a much lower feeding rate for COTS (hence less damage per COTS/coral area). This highlights that latitudinal and seasonal differences in coral-COTS dynamics could depend on COTS feeding rates as much as coral growth and that future analyses may need to consider the double effect of sea surface temperature (SST) on COTS feeding and coral growth rates.

6.1.2 Efficacy of COTS control on coral cover

Ideally, a before-after-control-impact (BACI; or similar) study (e.g. Pitcher et al. 2009) would contribute to our understanding of COTS control on coral trajectories. An empirical BACI analysis should be a priority for future COTS GBR control work and could potentially be achieved by leveraging and combining multiple sources of data (e.g. Kroon et al. 2021) such as the AIMS Long-Term Monitoring Program data and recent IPM COTS Control Program. Coral communities are dynamic, as are COTS and COTS outbreaks. Moreover, COTS control varies regionally and temporally in response to these dynamics and evaluation of outcomes requires careful consideration to avoid confounding effects. Based on our modelling, it is strongly recommended that care is taken in how to define “control” sites (or reefs) and how well they are likely to track an impact site where COTS management takes place. The present modelling suggests that the signal of COTS control is heterogenous depending on local factors and sensitive to perturbation (bleaching). This may modify the timing and spatial extent of different outbreaks (e.g. low coral cover constrains COTS abundance). The 2016 and 2017 bleaching events have also been suggested by Westcott et al. (2020) to have reduced the full benefit of COTS control in terms of coral cover. A BACI analysis would provide additional insight into how COTS control influences coral cover trajectories.

6.1.3 Expanding the reef-scale MICE

Manual culling of COTS is one way for coral reef managers to influence coral cover trajectories on the GBR. It can however only be scaled to the extent that is possible given available resources, COTS dynamics (e.g. outbreaks), and coral cover. In this project, we expanded on the existing model of Rogers and Plagányi (2022) to (1) include greater spatial coverage of the GBR, (2) fit the latest available data on COTS and corals, (3) include large fish predators of COTS, and (4) propose a framework to include mechanistic behavioural responses of COTS in relation to coral availability and predation risk. These developments extend the geographical footprint of the model which now includes reefs between Cairns and

Townsville and additional reefs in the Capricorn and Bunker, and Swains groups, and captures the potential role of predators alongside manual control. In the future, including potential behavioural response of COTS to coral and predator dynamics should be investigated as it applies to management. For example, described behavioural features of COTS (e.g. homing behaviour; Ling et al. 2020) and indirect interactions, such as predator-induced cryptic behaviour (e.g. urchins; Spyksma et al. 2017; Smith and Tinker 2022) are yet to be investigated for COTS, but could impact COTS detectability and ability to be culled. There is also related work on semiochemicals to support novel COTS management control (Motti et al. 2022). Combining these aspects into a tactical COTS management framework that is formally fitted directly to management data, would allow for the day-to-day performance of management to be modelled and for their likely outcomes to be characterised (such as coral saved at the reef or sub-reef scale). The tactical ecosystem model we have developed here and built on will also be useful to identify where, and how, current COTS management may be sensitive to alternative approaches to COTS control (e.g. fish predator management) and identify where further empirical work may be needed.

Future model development may be able to separate the preferred coral group (i.e. fast-growing corals) in the MICE more finely, but this will depend on data availability and quality. Data on coral composition at sites was only available from the RHIS data. The RHIS data splits coral composition into several morphologically based groups. To inform the model, it was necessary to assume what corals these morphologies related to and which model group they aligned with; the aggregated groups were subsequently used to assist model fitting. The current model uses a preferred fast-growing coral group which includes plate, table, branching, and bushy corals. Bushy and foliose corals could be important morphological groups to COTS during their early life history (Wilmes et al. 2020). Model development and expansion of early life history stages may require further delineation of preferred coral prey by splitting bushy and foliose coral species into their own group to model their interactions with juvenile coral-feeding COTS. Each RHIS only captures a small area of a control site (Beeden et al. 2014) and formal model fitting of the expanded MICE suggests that manta-based total coral cover metrics, which cover a larger area, are likely to be more reliable (less variable) than the RHIS measures. The capacity to introduce an additional coral group, that is fitted to data, would require continued collections of both manta-based coral cover measures and RHIS measures to ensure that inferences are reliable.

To fit the MICE to the manta data from the Control Program, it was necessary to assume the midpoints of coral cover categories. Assuming midpoints is not ideal and alternatives were investigated. Employing midpoints has the potential to over or underestimate data and there may be too few observations to assume observations falling within a category converge to their midpoint, nor is it able to capture the potentially heteroskedastic behaviour of cover data at bounded domain endpoints (Damgaard and Irvine 2019). An approach that does not rely on assigning a particular value would be ideal such that a point could equally be near the category upper or lower bound where the likelihood is informed by temporal correlation in the series. We however found that the relevant distributions needed to first be characterised or prespecified (e.g. its dispersion/variability) such that maximum likelihood methods (to fit the model) could be applied. As we did not have a basis upon which we could support such an assumption, we used more standard methods (e.g. Plagányi and Butterworth 2012; Tulloch et al. 2018) in conjunction with midpoints (Kroon et al. 2021) to fit the MICE. If the dispersion and variability of ‘true’ coral cover values and their assigned category were characterised (i.e. how often is x % coral cover assigned to each ordinal coral cover category), terrestrial approaches employed for plant cover may be applicable (e.g. the

Beta distribution; Damgaard and Irvine 2019) to aid in the inference and fitting of coral cover data. The development of approaches based on the Beta distribution may also provide a framework through which fine scale pinpoint data can be analysed alongside data from broader transect data which may help to link RHIS and manta-based data.

In summary, the outputs from this project specifically benefit the COTS Control Program as follows:

- The expansion of the coral-COTS MICE to incorporate and fit more reefs and management sites, plus a model framework for including predation on COTS, as a platform for future modelling of synergism between the COTS Control Program and potential indirect management levers such as fish predator abundance.

- The application of the MICE to estimate coral cover benefit by comparing current COTS control vs historical approach vs no control allows the COTS Control Program to tailor a more efficient and effective operational response.

- Assessing the cost vs benefit of refining COTS thresholds based on coral cover (Effort Sinks) or applying different thresholds depending on objectives (e.g. ecological threshold vs fertilisation threshold) can translate into both a more efficient and effective control response as well as improved detection and monitoring.

All of these ultimately contribute to the impacts the CCIP aimed to achieve, namely that COTS outbreaks are suppressed and prevented, coral cover is protected across the GBR, and Traditional Owners, tourism industry and the community benefit.

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8. DATA ACCESSIBILITY

Model output files can be made available on request from the authors. Raw data for the COTS Control Program are available under a Creative Commons license (CC BY-NC 4.0) through the Great Barrier Reef Marine Park Authority (email: cotsprogram@gbrmpa.gov.au).

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10. APPENDICES

APPENDIX A CORAL COVER DATA

Manta tow coral cover data

Unlike the RHIS or COTS culling data, the manta tow data makes use of ordinal categories which define an interval for coral cover observed on a manta tow. Due to the use of ordinal categories, typical approaches (e.g. Plagányi and Butterworth 2012; Morello et al. 2014; Tulloch et al. 2018; Rogers and Plagányi 2022) that fit the model to point-wise data were not considered most appropriate as the unobserved true coral cover value could have been anywhere on the interval defined by the category. However, difficulty was encountered when applying maximum likelihood methodology to resulting objective function contributions that would allow for analytical calculation of parameters at the maximum likelihood estimate. We found it necessary that some assumptions would have needed to have been made around the variance and dispersion of the distribution that related the model predictions to the true unobserved coral cover values. As we did not have a basis upon which to inform such assumptions, we instead opted to use category midpoints (e.g. Kroon et al. 2021) as they did not require this. The drawback of using midpoints is the potential for over or underestimation of the true coral cover value, however as the model and the data are free to inform the shape of the distribution (we do not assume the variance), points where this occurs will be implicitly weighted as less reliable and inform the model to a smaller degree.

Appendix Table 1 Coral cover categories from the Crown-of-thorns starfish Control Program manta tow data. Categories are the ordinal categories recorded during observations, “lower” indicates the lower bound in coral cover % of the category, “upper” indicates the upper bound in coral cover % of the category, and “midpoint” is the middle % value in the range for the coral cover category. The midpoint is assumed for model fitting.

Manta Coral Category	Lower (%)	Upper (%)	Midpoint (%)
0	0	0	0
1-	1	5	3
1+	6	10	8
2-	11	20	15.5
2+	21	30	25.5
3-	31	40	35.5
3+	41	50	45.5
4-	51	62	56.5
4+	63	75	69
5-	76	87	81.5
5+	88	100	94

RHIS coral cover data

We primarily used RHIS for composition information as it allowed for greater taxonomic inference of corals as they relate to COTS dynamics. Given the current model structure, assumptions were required around how to aggregate the coral types as they relate to COTS feeding preferences and growth rate on the GBR (**Appendix Table 2**). It was necessary to retain all coral groups (in aggregating) to ensure that implicit total coral cover was compatible with the manta tow hard coral cover. Branching, bushy, plate, and table corals were considered preferred prey items and to have a fast growth rate. Massive and mushroom corals were considered non-preferred prey items and have a slow growth rate. Vase, foliose, and encrusting corals have a typically moderate growth rate, and these were assigned to the non-preferred slow growing coral category because they are non-preferred prey items for COTS. RHIS supplemented the manta data for informing model coral cover.

Appendix Table 2 Allocation of Reef Health Impact Survey (RHIS) coral morphological types to crown-of-thorns starfish (COTS) feeding preference and growth rate based on assumed characteristic types on the GBR.

RHIS coral morphology descriptor	Common types on the GBR	Allocated model group: 1 - Preferred-fast growing; 2 - non-preferred slow growing
Branching coral	Acroporidae, Pocilloporidae	1
Bushy coral	Acroporidae, Pocilloporidae	1
Plate/table coral	Acroporidae	1
Vase/foliose coral	Agaricidae, *Montipora*, Acroporidae	2
Encrusting coral	Siderastreidae, *Montipora* Acroporidae	2
Massive coral	Faviidae, Poritidae, Merulinidae, Siderastreidae	2
Mushroom coral	Fungiidae	2

Potential non-COTS perturbations

COTS are one source of mortality on coral reefs and other leading causes of coral mortality include severe storms and cyclones as well as coral bleaching (De'ath et al. 2012). To identify potential sources of coral mortality that were not COTS related, the AIMS data portal (https://apps.aims.gov.au/reef-monitoring/reefs) was used to identify whether cyclone(s) and/or bleaching event(s) had occurred at a reef between 2018 and 2021 that would need to be accounted for and attributed during model fitting. Not all reefs were assessable through the data portal and AIMS sector-specific reports (https://www.aims.gov.au/research-topics/monitoring-and-discovery/monitoring-great-barrier-reef/reef-reports-hub) were used as supplementary information on whether bleaching was a likely impact. The Bureau of Meteorology past tropical cyclone reports (http://www.bom.gov.au/cyclone/tropical-cyclone-knowledge-centre/history/past-tropical-cyclones/) provided information about whether a tropical cyclone (or low) may have impacted one of the listed reefs (assumed to be a track within ~100 km of a chosen reef) (**Appendix Table 3**).

Appendix Table 3 Summary of potential non-COTS mortality sources for reefs included for model fitting between mid-2018 and mid-2021. Sources of information are the AIMS data portal (AIMS), Bureau of Meteorology past tropical cyclone reports (BOM), and the AIMS annual reports.

Reef name	**Cyclone (AIMS)**	**Bleaching event (AIMS)**	**Possible cyclone or low (BOM)**	**Indicative nominal bleaching level (AIMS reports)**			
				2021	2020	2019	2018
Fitzroy Island Reef (No 1)			2018 (Owen), 2021 (Kimi)	Low	Mod		Low
U/N Reef (16-054f)			2018 (Owen), 2021 (Kimi)	Low	Mod		Low
Moore Reef			2018 (Owen), 2021 (Kimi)	Low	Mod		Low
Normanby-Mabel Reef			2021 (Kimi)	Low	Mod	Low	Low
Round-Russell Reef			2021 (Kimi)	Low	Mod	Low	Low
Eddy Reef			2021 (Kimi)	Low	Mod	Low	Low
Farquharson Reef			2021 (Kimi)	Low	Mod	Low	Low
Britomart Reef			2021 (Kimi)	Low	Mod	Low	Low
Trunk Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Bramble Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Fore And Aft Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
John Brewer Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Keeper Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Lynchs Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Davies Reef			2021 (Kimi)	Low	Low–Mod	Low	Low
Big Broadhurst Reef (No 1)				Low	Low–Mod	Low	Low
Obstruction Reef				Low	Low		Low
U/N Reef (21-557)				Low	Low		Low
U/N Reef (22-084)				Low	Low		Low
Horseshoe Reef (No 1)				Low	Low		Low
Heron Reef				Low	Low		Low
Fitzroy Reef				Low	Low		Low
Llewellyn Reef				Low	Low		Low
Boult Reef				Low	Low		Low
Hoskyn Islands Reef				Low	Low		Low
Fairfax Islands Reef				Low	Low		Low
Lady Musgrave Reef				Low	Low		Low
Lady Elliot Island Reef		2020		Low	Low		Low

APPENDIX B SHORTLISTING REEFS FOR MODELLING

The entire set of reefs was not modelled. Reefs were initially included for modelling if they had one or more sites that had been visited for culling six or more times; some reefs were also requested for inclusion by the Great Barrier Reef Marine Park Authority (GBRMPA) and our criteria were also applied to these. If a reef was shortlisted, then only sites on that reef with at least six control visits were included. Filtering reefs and sites was necessary as many reefs and sites had been visited infrequently (e.g. once) between 2018 and 2021. In total, there were a total of 28 reefs and 234 sites that met our criteria. Of the reefs requested by the GBRMPA it was not possible to fit the model to sites on Batt Reef and Wheeler Reef, as these had not been visited enough at the time of writing. Shortlisted reefs and the rationale behind their selection are provided in **Appendix Table 4** and a map of reef locations is in provided in **Figure 4**.

Appendix Table 4 Summary of initial shortlisted reefs, rationale for their inclusion, and the number of sites on the reef for which data were available.

Name	Number	Requested (Yes/No)?	Number of sites
Fitzroy Island Reef (No 1)	16-054a	No	1
U/N Reef (16-054f)	16-054f	No	3
Moore Reef	16-071	No	2
Normanby-Mabel Reef	17-012	Yes	2
Round-Russell Reef	17-013	Yes	4
Eddy Reef	17-047	No	10
Farquharson Reef	17-063a	No	9
Britomart Reef	18-024	No	4
Trunk Reef	18-027	No	26
Bramble Reef	18-029	No	13
Fore And Aft Reef	18-043	No	15
John Brewer Reef	18-075	No	32
Keeper Reef	18-079	No	18
Lynchs Reef	18-091	No	5
Davies Reef	18-096	No	5
Big Broadhurst Reef (No 1)	18-100a	Yes	6
Obstruction Reef	21-552	No	2
U/N Reef (21-557)	21-557	No	1
U/N Reef (22-084)	22-084	No	6
Horseshoe Reef (No 1)	22-104a	No	5
Heron Reef	23-052a	No	2
Fitzroy Reef	23-077	No	16
Llewellyn Reef	23-078	No	6
Boult Reef	23-079	No	7
Hoskyn Islands Reef	23-080	No	2
Fairfax Islands Reef	23-081	No	5
Lady Musgrave Reef	23-082a	No	25
Lady Elliot Island Reef	24-008	No	2

APPENDIX C LIKELIHOOD EQUATIONS AND CONTRIBUTIONS

The full model details are described in Rogers and Plagányi (2022), and in this report we restrict presentation to new equations needed to fit the updated model to new data. Tables 5–7 show the variables and equations used in the maximum likelihood estimation approach. The programming language, Automatic Differentiation Model Builder (ADMB), was used to develop and fit the model. ADMB uses a quasi-newton optimalisation algorithm to estimate parameters and Hessian based standard deviations (Fournier et al. 2012).

Appendix Table 5 Variables and definitions employed in the maximum likelihood estimation approach for model fitting.

Variable	Name	Description
$CPUE_i$	Model catch-per-unit-effort	Model predicted catch-per-unit-effort for a given site on a reef on a given day in a particular year.
C_i^T	Model total coral cover	Model predicted total coral cover for a given site on a reef on a given day in a particular year.
C_i^G	Model coral cover of group G (fast or slow growing)	Model predicted coral cover of a given type (fast or slow) for a given site on a reef on a given day in a particular year.
$\widehat{CPUE_i}$	Observed catch-per-unit-effort	Observed catch-per-unit-effort for a given site on a reef on a given day in a particular year.
$\widehat{C_i^T}$	Observed total coral cover	Observed total coral cover for a given site on a reef on a given day in a particular year.
$\widehat{C_i^G}$	Observed coral cover of group G (fast or slow growing)	Observed coral cover of a given type (fast or slow) for a given site on a reef on a given day in a particular year.
n_{CoTS}^{CULL}	Number of catch-per-unit-effort observations	Number of catch-per-unit-effort observations at a site over the duration of data period.
n_{coral}^{MANTA}	Number of total coral cover observations	Number of manta tow coral cover observations at a site over the duration of data period.
n_{coral}^{RHIS}	Number of coral group observations	Number of observations of coral cover of a given type (fast or slow) at a site over the duration of the data period.
$r_{y,rf}^{rec}$	Recruitment residuals	Fitted crown-of-thorns starfish recruitment variation for a reef each year.

r_{site}^{CM}	Catch magnitude deviations	Deviation between modelled crown-of-thorns starfish catches by the control program and those suggested by the model.

Appendix Table 6 Parameter, their value(s), and definition or source (where applicable) employed in the maximum likelihood estimation approach for model fitting.

Parameter	Value	Description/source
δ_{CoTS}	0.0001	Small term applied to catch-per-unit-effort rates to ensure logarithm domains are not violated.
δ_{coral}	0.01	Small term applied to both observed coral cover and modelled coral cover to ensure condition that both $\delta_{coral} + \widehat{C_i^G} > 0$ and $\delta_{coral} + \widehat{C_i^G} > 0$.
σ_R	0.70	Rogers and Plagányi (2022)
σ_{CM}	0.10	Rogers and Plagányi (2022)

Appendix Table 7 Overview of likelihood components and penalty terms that contribute to the model fitting objective function.

Name	Equation	No.
Objective function	$f_{obj} = -\log\mathrm{L}_{CULL} - \log\mathrm{L}_{MANTA} - \log\mathrm{L}_{RHIS} - \log\mathrm{L}_{SRP} - \log\mathrm{L}_{CM}$	1
Negative log-likelihood contributions from a site for catch-per-unit-effort data	$-\log\mathrm{L}_{CULL} = n_{CoTS}^{CULL}\ln(\sigma_{CULL}) + \sum_{i=1}^{n_{CoTS}^{CULL}} \frac{\left(\ln(\delta_{CoTS} + \widehat{CPUE_i}) - \ln(q_{site}(\delta_{CoTS} + CPUE_i))\right)^2}{2{\sigma_{CULL}}^2}$	2a

Name	Equation	No.
Negative log-likelihood contributions from a site for manta tow coral cover data	$-\log\mathrm{L}_{MANTA} = \sum_{i=1}^{n_{coral}^{MANTA}} \ln\left(\frac{\sigma_{MANTA}}{\sqrt{\widehat{C_i^T}}}\right) + \frac{\left(\ln\left(\delta_{coral} + \widehat{C_i^T}\right) - \ln\left(\delta_{coral} + C_i^T\right)\right)^2}{2\sigma_{MANTA}{}^2}$	2b
Negative log-likelihood contributions from Reef Health Impact Surveys for fast and slow growing coral cover at a site	$-\log\mathrm{L}_{RHIS} = \sum_{i=1}^{n_{coral}^{RHIS}} \sum_{G=\{F,S\}} \left[\ln\left(\frac{\sigma_{RHIS}}{\sqrt{\widehat{C_i^G}}}\right) + \frac{\left(\ln\left(\delta_{coral} + \widehat{C_i^G}\right) - \ln\left(\delta_{coral} + C_i^G\right)\right)^2}{2\sigma_{RHIS}{}^2}\right]$	2c
Standard deviation for CPUE data at a site	$\sigma_{CULL} = \sqrt{\frac{1}{n_{CoTS}^{CULL}} \sum_{i=1}^{n_{CoTS}^{CULL}} \left(\ln\left(\delta_{CoTS} + \widehat{CPUE_i}\right) - \ln\left(q_{site}\left(\delta_{CoTS} + CPUE_i\right)\right)\right)^2}$	3a
Standard deviation for manta coral cover data at a site	$\sigma_{MANTA} = \sqrt{\frac{1}{n_{coral}^{MANTA}} \sum_{i=1}^{n_{coral}^{MANTA}} \left(\ln\left(\delta_{coral} + \widehat{C_i^T}\right) - \ln\left(\delta_{coral} + C_i^T\right)\right)^2}$	3b
Standard deviation for RHIS coral cover (fast and slow coral) data at a site	$\sigma_{RHIS} = \sqrt{\frac{1}{n_{coral}^{RHIS}} \sum_{i=1}^{n_{coral}^{RHIS}} \sum_{G=\{F,S\}} \left(\ln\left(\delta_{coral} + \widehat{C_i^G}\right) - \ln\left(\delta_{coral} + C_i^G\right)\right)^2}$	3c
Crown-of-thorns starfish catchability parameter	$q_{site} = \exp\left(\frac{1}{n_{CoTS}^{CULL}} \sum_{i=1}^{n_{CoTS}^{CULL}} \ln\left(\delta_{CoTS} + \widehat{CPUE_i}\right) - \ln\left(\delta_{CoTS} + CPUE_i\right)\right)$	4

Parameter(s)	Values
Coral growth rate reductions (r_{red}^{f}, r_{red}^{m})	-10 %, -20 %, -30 %, -40 %, -50 %, -60 %, -70 %
Coral growth rate increases (r_{red}^{f}, r_{red}^{m})	10 %, 20%, 65 % (65 % used to proximate 10 CoTS.ha^{-1} given 82 % detectability at 35 % coral cover)
Fixed cover of fast-growing corals relative (C^{f}/K^{f}) for slow-growing coral calculations	20 %, 50 %, 80 %

Name	Equation	No.
Stock recruitment penalty	$-\log\mathrm{L}_{SRP} = \sum_{y=1}^{Years} \sum_{rf=1}^{Reefs} r_{y,rf}^{rec} \Big/ 2{\sigma_R}^2$	5a
Catch magnitude penalty	$-\log\mathrm{L}_{CM} = \sum_{site=1}^{Sites} r_{site}^{CM} \Big/ 2{\sigma_{CM}}^2$	5b

Appendix Table 1 Growth rate parameters considered for evaluation of the coral growth dynamics in Equation 2 (relative to parametrisation of Morello et al. (2014) and Plagányi et al. (2020) analysis).

APPENDIX D EQUILIBRIUM THRESHOLDS

Derivation of equilibrium thresholds

The current equilibrium thresholds used as targets for manual COTS control on the GBR are based on the MICE of Morello et al. (2014). The Morello et al. (2014) MICE is numerically solved to obtain approximations of the point at which COTS-coral interactions and associated impacts balance coral growth (Plagányi et al. 2020). This entails equating the population dynamics of encompassed (aggregated) coral groups and the effects of COTS-coral feeding interactions. Interactions in this formulation include variable coral growth depending on coral cover and density-dependent effects of COTS on coral dynamics. COTS are considered to feed on coral from age-1 ($N_{1,\infty}$) and are included alongside age-2+ COTS ($N_{2+,\infty}$) for computation of coral impacts. Coral mortality occurring due to bleaching or cyclones was not modelled nor was explicit predation mortality of COTS. Variable ΔC_∞^f denotes the annual expected difference in fast-growing coral as a percentage of its carrying capacity ($\Delta C_\infty^f = C_{y+1,\infty}^f - C_{y,\infty}^f$) considering coral growth and COTS effects. Within the subscript of variables, an ∞ denotes that calculations are computed for equilibrium (growth equals impact of COTS on fast-growing coral cover, ($\Delta C_\infty^f = 0.00$) or different specified steady states (e.g. COTS required to cause a 5 % loss in fast-growing coral cover, $\Delta C_\infty^f = -0.05$). Base dynamics for fast-growing corals are given by (Plagányi et al. 2020):

$$\Delta C_\infty^f = r^f \cdot \left(1 - C_\infty^f/K^f\right) \cdot \left(C_\infty^f/K^f\right) - \frac{p_1^f \cdot \left(N_{1,\infty} + N_{2+,\infty}\right) \cdot e^{\left(-5C_\infty^f/K^f\right)} \cdot \left(C_\infty^f/K^f\right)}{1 + e^{\left(-(N_{1,\infty}+N_{2+,\infty})/p_2^f\right)}} \qquad [D.1a]$$

And similarly for slow-growing corals:

$$\Delta C_\infty^m = r^m \cdot (1 - C_\infty^m/K^m) \cdot (C_\infty^m/K^m) - \frac{p_1^m \cdot \left(N_{1,\infty} + N_{2+,\infty}\right) \cdot (1 + e^{\left(-5C_\infty^f/K^f\right)}) \cdot (C_\infty^m/K^m)}{1 + e^{\left(-(N_{1,\infty}+N_{2+,\infty})/p_2^m\right)}} [D.1b]$$

In this report we examined how different coral growth rates change predicted equilibrium thresholds relative to values fitted and parametrised by Morello et al. (2014) to the Lizard Island AIMS LTMP data (years 1994 to 2011). To capture differences in coral growth, the growth rate parameter of fast-growing (r^f) and slow-growing (r^m) coral groups was scaled by a given proportion (defined below) to capture relative differences in coral growth. For a particular reduction or increase of r_{red}^f % for fast-growing and r_{red}^m % for slow-growing corals, growth and equilibrium dynamics were modelled through:

$$\Delta C_\infty^f = \left(r^f\left(100 + \left(r_{red}^f\right)\right)/100\right) \cdot \left(1 - C_\infty^f/K^f\right) \cdot \left(C_\infty^f/K^f\right) - \frac{p_1^f\left(N_{1,\infty} + N_{2+,\infty}\right) \cdot e^{\left(-5C_\infty^f/K^f\right)} \cdot \left(C_\infty^f/K^f\right)}{1 + e^{\left(-(N_{1,\infty}+N_{2+,\infty})/p_2^f\right)}} \qquad [D.2a]$$

$$\Delta C_{\infty}^{m} = \left(r^{m}\left(100 + (r_{red}^{m})\right)/100\right) \cdot (1 - C_{\infty}^{m}/K^{m}) \cdot (C_{\infty}^{m}/K^{m}) - \frac{p_{1}^{m} \cdot \left(N_{1,\infty} + N_{2+,\infty}\right) \cdot \left(1 + e^{\left(-5C_{\infty}^{f}/K^{f}\right)}\right) \cdot (C_{\infty}^{m}/K^{m})}{1 + e^{\left(-(N_{1,\infty}+N_{2+,\infty})/p_{2}^{m}\right)}} \qquad [D.2b]$$

For example, $r_{red}^{f} = -30$ would result in a 30 % relative reduction of r^{f} (i.e. $0.7 \times r^{f}$). Conversely, $r_{red}^{f} = 10$ would constitute a 10 % relative increase in r^{f} (i.e. $1.1 \times r^{f}$). Different growth rates considered within the present report were selected to cover reported changes (noting that this may be no change) in coral growth that may be associated with bleaching events and latitudinal differences (e.g. Cantin et al. 2010; Cantin and Lough 2014; Anderson et al. 2017). The levels of change modelled here do not preclude that more severe changes could occur. We did not consider the case of no coral growth (i.e. $r_{red}^{f} = -100$) as this would result in the trivial case of 0 COTS at equilibrium and CPUE of 0 COTS.min^{-1}. Considered coral growth rate changes are presented in **Appendix Table 8**. A Newton-Raphson root-finding was implemented to identify the requisite number of COTS to sustain a given change in coral cover ($\Delta C_{\infty}^{f}, \Delta C_{\infty}^{m}$) (Plagányi et al. 2020).

Translating the fertilisation threshold into a target catch rate

Here we translate the 3 COTS.ha^{-1} fertilisation threshold (Rogers et al. 2017) to the CPUE metric currently employed by the Control Program. This is done using the developed and formally fitted hyperstability relationship of Plagányi et al. (2020); the same way as COTS densities are converted to CPUE values for the ecological threshold. Conversion of the density estimate to a CPUE estimate allows for comparison of the fertilisation threshold to the nominal 0.04 COTS.min^{-1} and 0.08 COTS.min^{-1} CPUE targets currently in use (Babcock et al. 2014; Fletcher et al. 2020; Plagányi et al. 2020; Westcott et al. 2021b).

Catch rate (CPUE) is related to COTS density via the hyperstability relationship (Plagányi et al. 2020):

$$CPUE = q \cdot \left(N_{t}^{Cull}\right)^{h} \cdot \left({}^{1}/_{60}\right) \qquad [D.3]$$

Given that detectability, and in turn catch efficiency, varies with COTS size, the expected CPUE will depend on the demographic composition of the population. COTS can reach maturity towards the end of their second year (Lucas and Jones 1976; Zann et al. 1987). This nominally corresponds to the age-2+ class in the Plagányi et al. (2020) MICE formulation (age-1 COTS <150 mm diameter and age-2 COTS >150 mm diameter). We note that COTS are capable of reproduction at sizes consistent with ages 1+ (female 130 mm diameter Bos et al. 2013; male 120 mm diameter Pratchett et al. 2021). We do not consider these individuals in our study as they likely have a limited role in recruitment given reproductive capacity exponentially increases with size (Babcock et al. 2016; Pratchett et al. 2021). The fertilisation threshold is based on the density of reproductive individuals, and we define the CPUE using the density of age-2+ individuals expected to reach the 3 COTS.ha^{-1} threshold. This threshold does not incorporate the density of age-1 individuals and therefore the total combined density of age-1 and age-2+ individuals may exceed 3 COTS.ha^{-1}. As per Plagányi et al. (2020), the expected equilibrium (unfished/uncontrolled) composition of a controllable COTS population is given by:

$$N_t^{Cull} = \beta \cdot N_{1,\infty} + \alpha \cdot N_{2,\infty} \qquad [D.4]$$

Where β is the detectable proportion of age-1 COTS and α is the detectable proportion of age-2+ COTS on a reef. For a given density of age-2+ COTS the corresponding relative number of age-1 COTS (based on estimates of natural mortality (Morello et al. 2014)) required to sustain said age-2+ COTS density is computed by:

$$N_\infty = N_{2,\infty} \cdot e^M \qquad [D.5a]$$
$$N_{1,\infty} = N_{2,\infty}(e^M - 1) \qquad [D.5b]$$

Therefore, with $M = 2.56$ (Morello et al. 2014) and a target age-2+ COTS density of $N_{2,\infty} = 3$ the corresponding number of age-1 COTS is $N_{1,\infty} = 35.8$. Consequently, the required CPUE based on the base parametrisation of Plagányi et al. (2020) to achieve an age-2+ COTS density of 3 COTS.ha^{-1} is calculated via equation [D.3] to be:

$$CPUE = 0.669 \cdot (0.82 \times 3 + 0.19 \times 35.8)^{0.5} \cdot \left({}^{1}/_{60}\right) = 0.034 \text{ COTS/min} \ \ (\sim 2 \text{ COTS/hr})$$

In our subsequent modelling we use a CPUE of 0.03 COTS.min^{-1} as a proxy target for culling to below the fertilisation threshold. Typically control dives last 40 minutes GBRMPA 2017; Fletcher et al. 2020) which corresponds to an average of ~1.3 COTS.dive^{-1}. If each dive covers a 400 m by 5 m transect (0.2 ha) per individual dive (GBRMPA 2017) then a rough overall target density (rule of thumb) is no more than a total of 6–7 COTS.ha^{-1} including no more than 2 age-2+ COTS.ha^{-1} (note that this calculation uses base parameter values and equilibrium formulation). This underscores the importance of identifying and documenting the number of reproductively mature COTS—raw CPUE or pure density estimates (no age-size delineations) may obscure the reproductive potential of a population which may be important depending on management goals at a reef or site.

APPENDIX E SIMULATING COTS CONTROL

Simulated voyage capability

We modelled a single control vessel with four priority reefs which had 13 sites in total. The voyage and dive capability of a vessel was modelled similar to Condie et al. (2021). A vessel was able to conduct 20 voyages per year. Each voyage lasted 10 days and could conduct control on 9 of those days, the remaining day was assumed to be lost in transit time. On each 'control day' of a voyage, up to four dives could be conducted. Each dive was assumed to be 40 minutes. Voyages were assumed to be abandoned if there was a (simulated) cyclone with five days of the voyage.

Simplified decision tree

The simplified decision tree used as part of the operational strategy for COTS control (Fletcher et al. 2020) was coded for simulation within the COTS MICE (Rogers and Plagányi 2022). The coded algorithm for the simplified decision tree (**Figure 6**) involved representing manta tow surveillance to identify reef sites that needed control. All sites at a reef detected above the manta-perceived threshold were simulated to be controlled. The manta perceived threshold was either one COTS observed or one COTS feeding scar observed on a manta-tow. The number of COTS detected on manta tows was calculated from modelled age-2 and age-3+ COTS densities as per the density-manta relationship (and parametrisation) of Plagányi et al. (2020). Culling is also triggered if one or more feeding scars are detected. If COTS are missed on manta tows, triggering control based on feeding scars is reliable and reported to be highly effective at the 3 to 4 COTS.ha^{-1} level (Fletcher et al. 2020, Westcott et al. 2021b). We assumed that any sites with four or more age-2 and age-3+ COTS (the largest and most readily detected individuals) would produce feeding scars and trigger culling. Once all sites identified by manta tows were controlled to below the ecological CPUE threshold (closed), the next reef was chosen from the priority list. The first dive at the new reef was replaced with a manta tow to gain information on how COTS were distributed across the reef's sites. Once dives at a site commenced, manta tow information for that site was replaced by CPUE data. Threshold targets for COTS control are a CPUE of 0.04 COTS.min^{-1} if coral cover is <40 %, and 0.08 COTS.min^{-1} if coral cover is ≥40 % (Plagányi et al. 2020). Control efforts were focused on a single site until it was reduced to below the relevant threshold. The next site detected for control (by the manta tow) with the highest perceived levels of COTS was selected, or if all sites were now closed, the next reef was selected.

Comparison of decision tree with historical control approach (2013 to 2018)

We simulated the simplified decision tree currently used for COTS control and compared this to how control was conducted from 2013 to 2018. Historically, control focused on high priority sites (mostly important tourism locations) and on removing the most COTS at sites (Westcott et al. 2021b). The program from 2013 to 2018 was largely asset protection. The current program prioritises reefs that are economically (e.g. tourism) and ecologically (sources of coral or COTS based on connectivity modelling; Hock et al. 2016) important. The IPM COTS Control Program also controls whole reefs as opposed to individual sites; it protects reefs (and sites) where control is conducted but also tries to indirectly reduce the regional impact of COTS on corals.

Both the implemented control (“actual”) at the sites and the simulated decision tree (“decision tree”) were compared to a modelled case assuming no control had taken place (“no control”). That is, we evaluated what difference it would have made if the decision tree algorithm had been implemented over this past period. The difference between the actual and no control scenarios were considered to inform the difference that implemented control made to coral trajectories. The difference between the decision tree and no control scenarios was considered to inform the difference that using the decision tree might have made to coral trajectories had it been used over this period (noting it was not yet developed at the time). For the set of reefs used here, there were no cyclones and therefore no voyages were lost in the simulations.

Caveats

The MICE is fitted to control activities and their impact on coral trajectories from the central GBR. The impact of COTS on corals could be greater in the region south of Cairns where corals likely have slower growth rates (Anderson et al. 2017). While we found that the balance between COTS consumption and coral growth (equilibrium) are similar for coral cover < 30 % under different modelled coral growth scenarios, the consequence of high COTS numbers is increased rates of coral cover loss at above equilibrium levels (Rogers et al. 2024). Under such circumstances, the impact of culling COTS will likely be higher than currently suggested by the model. The higher impact of culling COTS where coral growth is slower is because local corals (at the site and reef scale) recover more slowly. The current MICE also does not capture the potential regional benefit of increasing coral cover and recruitment output. A given coral cover percent improvement at the site scale may belie its regional importance, especially in areas where coral growth might be slower.

APPENDIX F EFFORT SINK DEFINITION AND OVERVIEW

Overview

The term ‘Effort Sink’ was conceptualised by Rogers (2022) and Rogers et al. (2023), with further reference made in a previous CCIP-R-03 milestone report and presentation (e.g. see **Appendix Figure 1**). Here we provide further thoughts on Effort Sinks including: a definition of the term, what causes Effort Sinks, the implications thereof, and an illustrative example of Effort Sinks on the GBR (**Appendix Figure 2**).

What is an Effort Sink?

A location that consumes a large portion of a limited resource (“Effort”) that then cannot be used elsewhere (“Sink”) and impacts management outcomes across the set of locations that require management. An Effort Sink is fundamentally a function of resource constraints (implicitly, spatial dilution), management targets, and the ecological dynamics in question. Note Effort Sinks are not just a function of the ecological dynamics and are not just a function of the management dynamics; it is an emergent property of the integrated dynamics.

Specific to COTS management on the GBR an Effort Sink is defined as a reef (or even site) that uses up lots of control time that cannot then be used at other reefs and detrimentally impacts the coral outcomes across the set of locations prioritised for COTS control. Effort Sinks are emergent of the integrated management dynamics and coral-COTS dynamics. Effort Sinks are a function of the spatial dilution of control effort, the culling thresholds targeted, and both the coral and COTS population dynamics (**Appendix Figure 1**).

CCIP-R-03: Defining an effort sink

- **What is an effort sink?**
  - Reef/site that uses up lots of time that can’t then be used elsewhere
- **What is looks like?**
  - One reef/site dominating most of efforts
- **What causes it?**
  - Limited resources
  - Lots of CoTS
  - Low coral/CPUE targets

Appendix Figure 1 Effort Sink slide taken from Rogers, J. (Thursday 16th February 2023). Dynamic models to inform COTS intervention strategies at the reef-scale: COTS Control Innovation Program (CCIP-R-03). CCIP seminar series: Video link.

What does it look like?

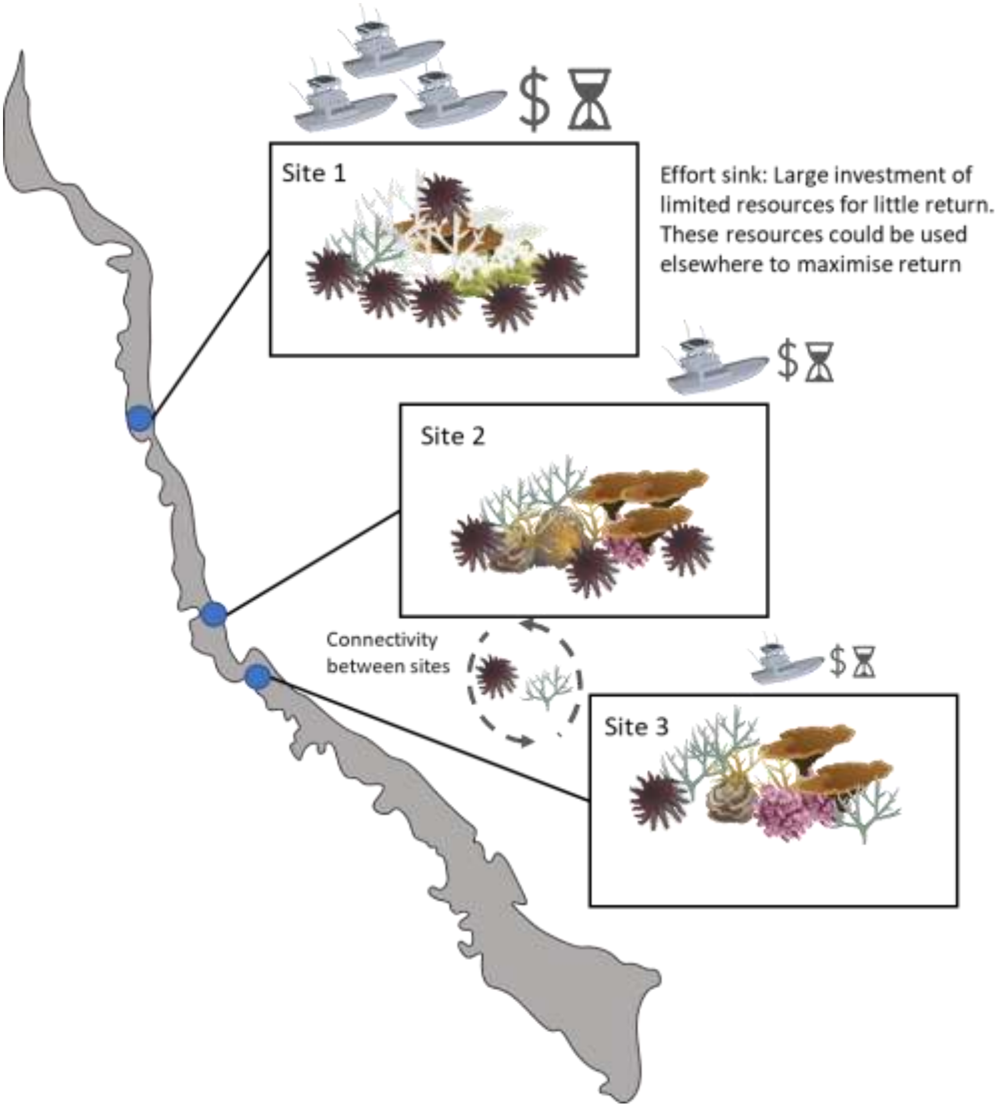
One reef or site dominating most of the control efforts. Outcomes from management become skewed towards this location (management metric median, e.g. coral cover, increasingly departs from the mean when looking at outcomes across the set of reefs or sites, namely the median is much smaller than the mean).

What causes Effort Sinks?

- Limited resources compared to the number of reefs that need control.
- Many COTS (and strong replenishment) at a small number of locations relative to the total number that are prioritised.
- Low coral cover which limits the immediate coral at the location that may be preserved and/or low CPUE targets which become more difficult to attain as COTS are culled.
- Absence of stopping rule(s) based on diminishing returns (i.e. quantification of when no longer cost-effective to continue at a location).

Implications of Effort Sinks

Inefficient distribution of resources. In general locations with less coral have lower CPUE targets to offset COTS consumption and they also have less coral to lose. The amount of coral saved per minute dive time (via COTS culled) may diminish and more coral area could potentially be managed by spreading cull resources, however care would be needed to avoid resource dilution. Exclusive of prioritisation factors related to reef identity, if a reef is considered to be in a very poor state, then it may be more beneficial to re-task culling efforts elsewhere based on the immediate coral that could be saved (e.g. **Appendix Figure 2**). The key trade-off that needs to be considered is Effort Sinks vs resource dilution which may be quantified in terms of the metric used to evaluate management performance, for example, mean coral cover or even possibly coral diversity.



Appendix Figure 2 Illustrative example of how an Effort Sink operates on the Great Barrier Reef. Effort could be sunk into one site for little coral cover return on that site (e.g. Site 1: coral cover already very low and COTS may eventually die out anyway), whereas there may be better outcomes if effort is targeted towards sites to maximise coral cover returns (e.g. Sites 2 and 3: coral reefs that are connected and still in fairly good health).

References cited in Appendix F:

Rogers J (2022) Developing a model of intermediate complexity for an Australian marine ecosystem: managing the crown-of-thorns starfish, *Acanthaster cf. solaris*. PhD Thesis, School of Mathematics and Physics, The University of Queensland. https://doi.org/10.14264/28fdbf3

- *Conceptualisation and defining of "Effort Sink".*

Rogers J, Plagányi É, Babcock R, Fletcher C, Westcott D (2023) Improving coral cover using an integrated pest management framework.

- *Manuscript in primary literature proceeding from PhD thesis (Note: discussions had with GBRMPA around manuscript prior to submission).*

Rogers J, Plagányi É, Blamey L, Desbiens A (2022) Comparison of intervention strategies for COTS control operations across the Great Barrier Reef: Simplified decision tree and historical implementation efficacy. CCIP progress report.

- *Presence of Effort Sink dynamics under modelling of Simplified Decision Tree approach.*

Rogers J. (Thursday 16th February 2023). Dynamic models to inform COTS intervention strategies at the reef-scale: COTS Control Innovation Program (CCIP-R-03). CCIP seminar series: Video link.

- *Public presentation of Effort Sinks to CCIP group.*

Details:

Rogers et al. (2023) Improving coral cover using an integrated pest management framework

Integrated pest management (IPM) leverages our understanding of ecological interactions to mitigate the impact of pest species on economically and/or ecologically important assets. It has primarily been applied in terrestrial settings (e.g. agriculture), but rarely been attempted for marine ecosystems. The crown-of-thorns starfish (COTS), *Acanthaster* spp., is a voracious coral predator throughout the Indo-Pacific where it undergoes large population increases (irruptions), termed outbreaks. During outbreaks COTS act as a pest species and can result in substantial coral loss. Contemporary management of COTS on the Great Barrier Reef (GBR) has recently adopted facets of the IPM paradigm to manage these outbreaks through strategic use of direct manual control (culling) of individuals in response to ecologically-based target thresholds. There has, however, been limited quantitative analysis of how to optimise the use of such thresholds. Here we use a multispecies modelling approach to assess the performance of alternative COTS management scenarios for improving coral cover trajectories. Scenarios examined varied in terms of their ecological threshold target, the sensitivity of the threshold, and level of management resourcing. Our approach illustrates how to quantify multi-dimensional trade-offs in resourcing constraints, concurrent COTS and coral population dynamics, stringency of target thresholds, and the geographical scale of management outcomes (number of sites). We found strategies with low target density thresholds for COTS (≤0.03 COTS.min^{-1}) could act as what we define as Effort Sinks and limit the number of sites that could be effectively controlled, particularly under COTS population outbreaks. This was because a handful of sites took longer to control which meant other sites were not controlled. Higher density thresholds (e.g. 0.04–0.08 COTS.min^{-1}), tuned to levels of coral cover, diluted resources amongst sites but were more robust to resourcing constraints and pest population dynamics. Our study highlights trade-off decisions when using an IPM framework and is informing implementation of threshold-based strategies on the GBR.

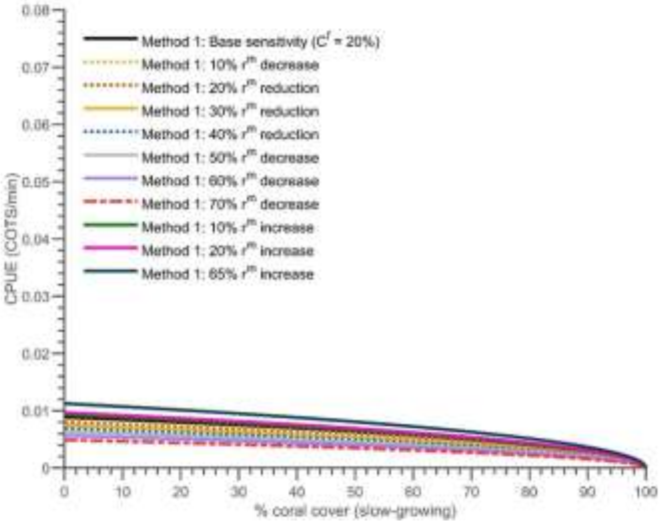
Effort sinks (Rogers 2022; Rogers et al. 2023):

The use of threshold-based approaches is subject to the creation of 'Effort Sinks' at relatively high-risk management sites (high COTS densities, potentially low coral cover). Effort sinks attract large and disproportionate amounts of management resources (substantially beneficial for said site), but most other sites also in need of control attract limited to no control effort (i.e. fewer locations are able to be controlled). The outcome is skewed improvements in coral cover and CPUE trajectories across sites.

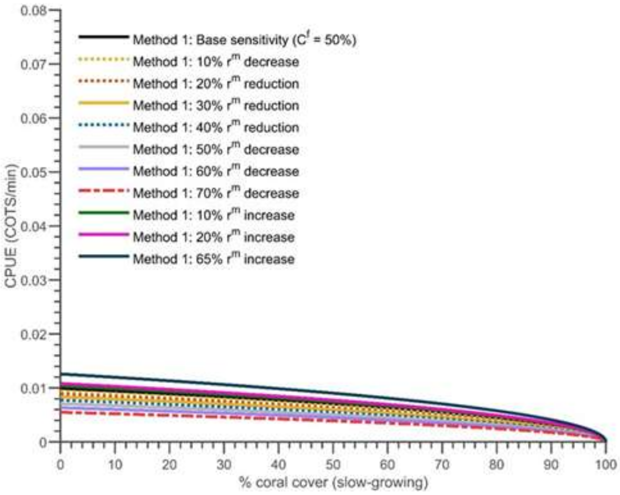
Factors influencing Effort Sinks (Rogers 2022; Rogers et al. 2023):

Effort Sink dynamics and their impact on management outcomes are a function of (1) available resources for a given set of locations, (2) COTS and coral dynamics, and the (3) specific thresholds used for culling COTS. Effort Sinks can emerge when there is a mismatch between the metrics used to assess performance (e.g. mean vs median), resources available to support management, and the spatial scale at which management is assessed. Resource limitations (fewer voyages) meant that there was less effort available for control and increased the strength of Effort Sinks. High COTS recruitment and low threshold targets (e.g. Allee-based threshold under outbreak conditions) also created strong Effort Sinks. Strong Effort Sinks have a relatively negative impact on coral cover outcomes; sufficient resourcing—given COTS dynamics—is critically important to attain ecologically meaningful outcomes, especially where other perturbations may play a large role and impact the corals that benefit most from COTS culling (e.g. fast-growing corals under bleaching events, Rogers and Plagányi 2022).

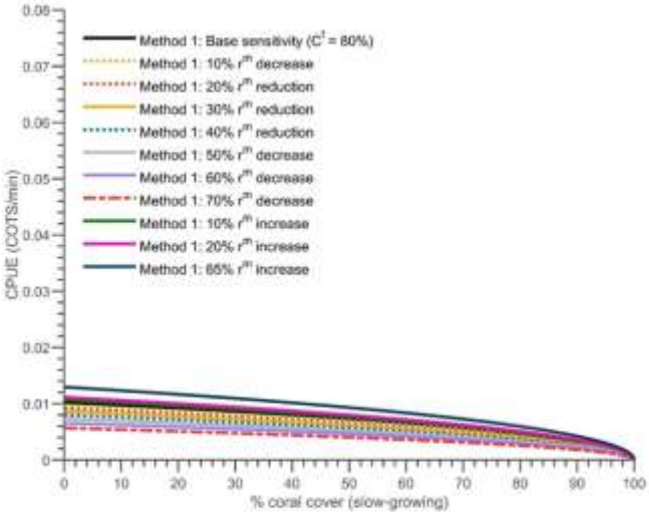
APPENDIX G REFINING ECOLOGICAL THRESHOLDS RESULTS



Appendix Figure 3 Expected catch-per-unit-effort (CPUE) for the Control Program against depletion level of slow-growing coral prey. Lines indicate the point at which the effects of COTS predation equilibrate the growth capacity of fast-growing corals. Different line colours and styles indicate alternative coral growth values relative to the parametrisation employed by Plagányi et al. (2020). Cover of fast-growing coral was fixed at 20 %.



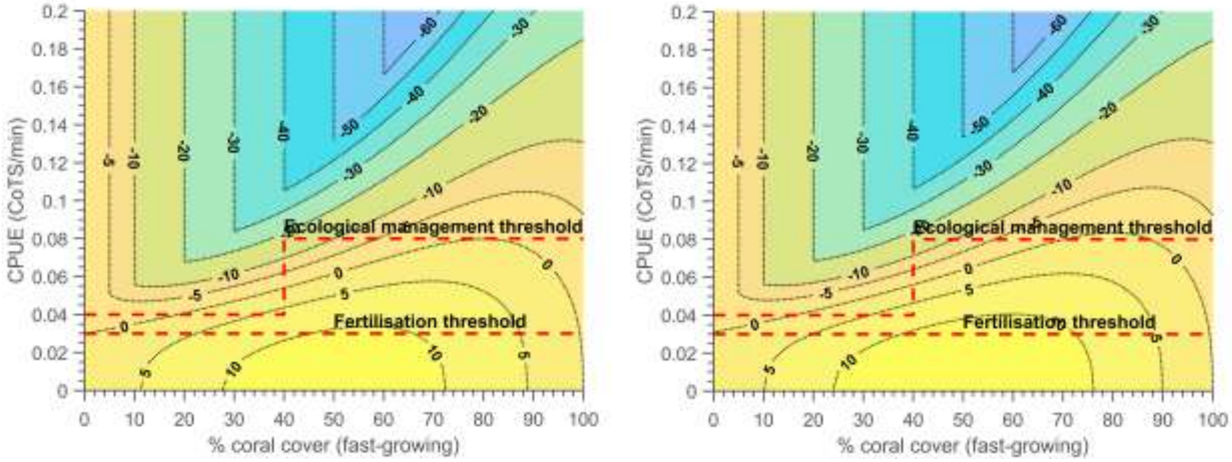
Appendix Figure 4 Expected catch-per-unit-effort (CPUE) for the Control Program against depletion level of slow-growing coral prey. Lines indicate the point at which the effects of COTS predation equilibrate the growth capacity of fast-growing corals. Different line colours and styles indicate alternative coral growth values relative to the parametrisation employed by Plagányi et al. (2020). Cover of fast-growing coral was fixed at 50 %.



Appendix Figure 5 Expected catch-per-unit-effort (CPUE) for the Control Program against depletion level of slow-growing coral prey. Lines indicate the point at which the effects of COTS predation equilibrate the growth capacity of fast-growing corals. Different line colours and styles indicate alternative coral growth values relative to the parametrisation employed by Plagányi et al. (2020). Cover of fast-growing coral was fixed at 80 %.

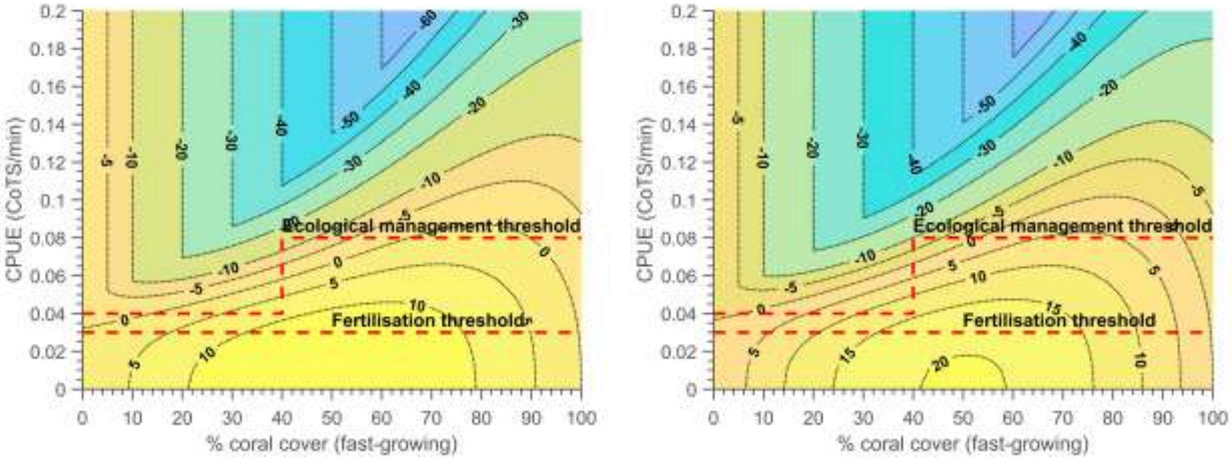
(a) 0 % difference

(b) 10 % increase



(c) 20 % increase

(d) 65 % increase



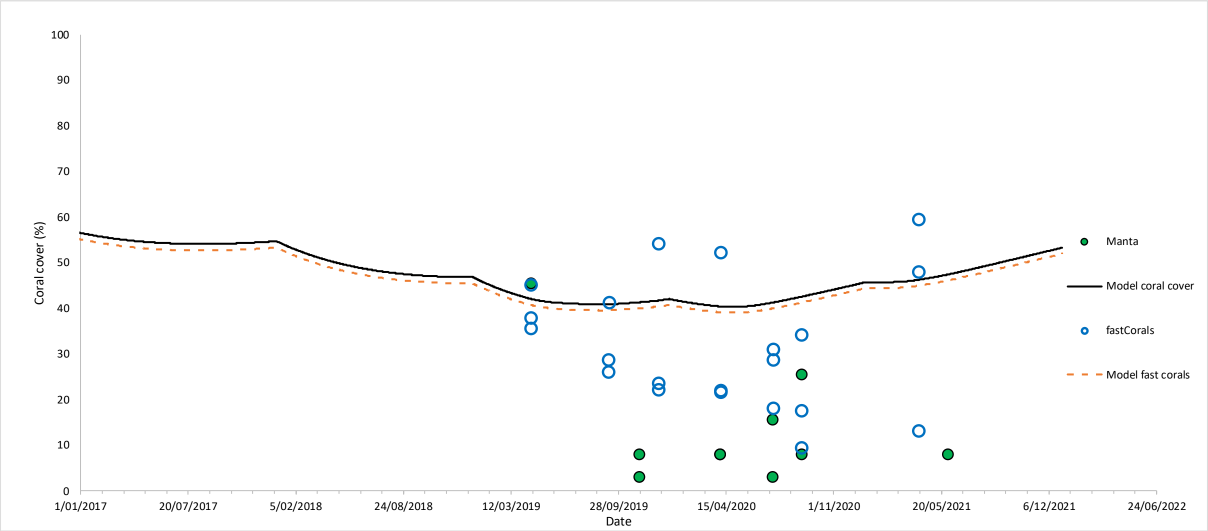
Appendix Figure 6 (a) Base case 0 % difference in fast-growing coral growth rate (Plagányi et al. 2020) included here as an index figure for reference, **(b)** 10 % increase in fast-growing coral growth relative to base case, **(c)** 20 % increase in fast-growing coral growth relative to base case, **(d)** 65 % increase in fast-growing coral growth relative to base case. See Box 1 for assistance with plot interpretation.

APPENDIX H MICE MODEL FITS

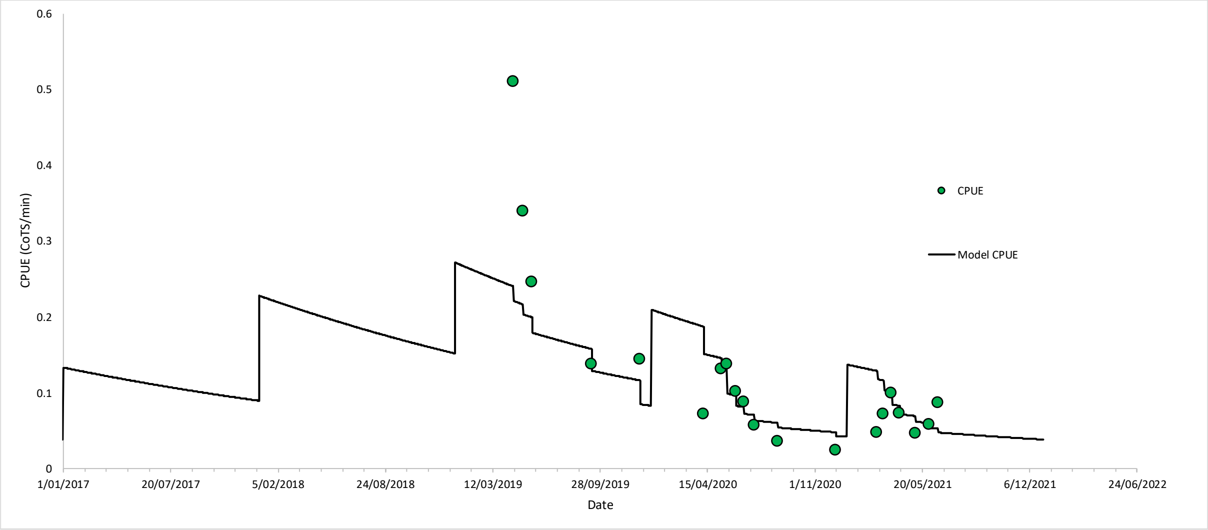
Appendix Table 9 Parameters estimated in the model along with the associated standard deviation (SD) and coefficient of variation (CV). Parameter P1_fast denotes the fast-growing coral feeding rate, parameters defined by format “CoTS_Recruitment_Variability_YEAR_REEF” denote the recruitment residuals for a given year for a given reef, parameters defined by format “CoTS_Recruitment_SITE” denote the annual COTS recruitment rate for a given site. The feeding rate was fitted common to all reefs, the recruitment residuals were fitted common to sites at the same reef for a given year, and the COTS recruitment rate was fitted at the site level.

Parameter name	Value	SD	CV
P1_fast	1.574E-06	7.181E-08	0.05
CoTS_Recruitment_Variability_2017_1	0.069	0.633	9.12
CoTS_Recruitment_Variability_2018_1	2.074	0.464	0.22
CoTS_Recruitment_Variability_2019_1	-0.664	0.529	0.80
CoTS_Recruitment_Variability_2020_1	-1.639	0.465	0.28
CoTS_Recruitment_Variability_2017_2	3.417	0.632	0.18
CoTS_Recruitment_Variability_2018_2	-1.057	0.590	0.56
CoTS_Recruitment_Variability_2019_2	-1.992	0.554	0.28
CoTS_Recruitment_Variability_2020_2	-1.493	0.606	0.41
CoTS_Recruitment_Variability_2017_3	-0.435	0.596	1.37
CoTS_Recruitment_Variability_2018_3	0.755	0.345	0.46
CoTS_Recruitment_Variability_2019_3	0.324	0.436	1.34
CoTS_Recruitment_Variability_2020_3	0.017	0.656	38.71
CoTS_Recruitment_Variability_2017_4	-1.064	0.508	0.48
CoTS_Recruitment_Variability_2018_4	2.562	0.190	0.07
CoTS_Recruitment_Variability_2019_4	1.630	0.203	0.12
CoTS_Recruitment_Variability_2020_4	0.514	0.522	1.01
CoTS_Recruitment_Variability_2017_5	0.431	0.575	1.33
CoTS_Recruitment_Variability_2018_5	0.545	0.462	0.85
CoTS_Recruitment_Variability_2019_5	0.326	0.313	0.96
CoTS_Recruitment_Variability_2020_5	-0.135	0.325	2.40
CoTS_Recruitment_Variability_2017_6	-0.437	0.557	1.28
CoTS_Recruitment_Variability_2018_6	-0.802	0.550	0.69
CoTS_Recruitment_Variability_2019_6	1.298	0.327	0.25
CoTS_Recruitment_Variability_2020_6	1.165	0.475	0.41
CoTS_Recruitment_Variability_2017_7	-0.125	0.606	4.83
CoTS_Recruitment_Variability_2018_7	0.238	0.410	1.72
CoTS_Recruitment_Variability_2019_7	-0.030	0.378	12.77
CoTS_Recruitment_Variability_2020_7	-0.800	0.495	0.62
CoTS_Recruitment_Variability_2017_8	-1.002	0.508	0.51
CoTS_Recruitment_Variability_2018_8	-0.346	0.457	1.32
CoTS_Recruitment_Variability_2019_8	2.509	0.261	0.10
CoTS_Recruitment_Variability_2020_8	3.169	0.303	0.10
CoTS_Recruitment_1	1804.700	669.320	0.37
CoTS_Recruitment_2	3979.000	1473.600	0.37
CoTS_Recruitment_3	239.880	142.910	0.60
CoTS_Recruitment_4	806.980	505.650	0.63

Parameter name	Value	SD	CV
CoTS_Recruitment_5	416.350	294.490	0.71
CoTS_Recruitment_6	527.240	333.430	0.63
CoTS_Recruitment_7	427.790	228.500	0.53
CoTS_Recruitment_8	310.640	87.377	0.28
CoTS_Recruitment_9	878.210	245.060	0.28
CoTS_Recruitment_10	2187.300	389.020	0.18
CoTS_Recruitment_11	888.570	155.780	0.18
CoTS_Recruitment_12	573.140	111.430	0.19
CoTS_Recruitment_13	1495.300	268.500	0.18
CoTS_Recruitment_14	1984.700	558.520	0.28
CoTS_Recruitment_15	2976.000	786.300	0.26
CoTS_Recruitment_16	1404.700	384.880	0.27
CoTS_Recruitment_17	319.560	94.045	0.29
CoTS_Recruitment_18	188.190	59.088	0.31
CoTS_Recruitment_19	380.180	116.890	0.31
CoTS_Recruitment_20	235.350	72.586	0.31
CoTS_Recruitment_21	421.940	131.320	0.31
CoTS_Recruitment_22	1101.800	340.900	0.31
CoTS_Recruitment_23	1585.500	438.350	0.28
CoTS_Recruitment_24	675.190	210.540	0.31
CoTS_Recruitment_25	3100.300	864.170	0.28
CoTS_Recruitment_26	4349.500	1330.100	0.31
CoTS_Recruitment_27	5653.700	1529.300	0.27
CoTS_Recruitment_28	232.080	78.535	0.34
CoTS_Recruitment_29	329.710	77.492	0.24
CoTS_Recruitment_30	233.040	55.443	0.24



Appendix Figure 7 Example model fit plot for coral cover (%) at Site 15 (Reef 5/Keeper Reef). Hollow blue circles are fast-growing coral observations from Reef Health Impact Surveys (RHIS) and solid green circles are total coral cover observations from the Crown-of-thorns starfish Control Program manta tows. The dashed orange line is the model-predicted coral trajectory of fast-growing corals and the solid black line is the model-predicted coral trajectory for total coral cover.



Appendix Figure 8 Example model fit plot for Crown-of-thorns starfish (COTS) Catch-Per-Unit-Effort (CPUE) rates (COTS.min^{-1}) at Site 15 (Reef 5/Keeper Reef). Green solid circles are CPUE rates from the COTS Control Program. Solid black line is the model-predicted CPUE trajectory.

APPENDIX I COMMUNICATION PIECES

Reef scale modelling: Bleaching & CoTS control

Coral bleaching and the coral predator, the crown-of-thorn starfish (CoTS), are leading causes of coral loss on the Great Barrier Reef. Culling CoTS is considered a direct way to limit coral loss but it is a costly and intensive process. Resources are limited to a handful of vessels which must prioritise reefs to manage. It is important to know how to use our resources effectively, especially with the increased number of bleaching events over the last few years. Here we summarise findings and inferences from recent work using Models of Intermediate Complexity for Ecosystem Assessment (MICE[1]) that have focussed on CoTS culling and coral bleaching. Recommendations are made based on the modelling work.

Bleaching limits CoTS control outcomes

Bleaching disproportionately impacts corals that would generally be protected by CoTS culling. These are typically faster growing coral species and culling following bleaching could expediate increasing coral cover at key locations (e.g. tourism sites, coral sources).

Promoting heat resilience potential

To give corals the best chance under thermal stress, our modelling suggests, reefs that experienced mild-severe bleaching and maintained coral cover >15-20% are likely important and a high priority. If coral cover is >15 % maintaining 0.04 CoTS/min, >40 %, 0.06 CoTS/min, and >60% then 0.08 CoTS/min could increase the likelihood a proportion of corals that survived the bleaching event persist given potential reductions in coral growth and recruitment. Nonetheless, it should be expected that some coral will still be lost but the decline won't be as great thereby increasing the likelihood of recovery and that next generation(s) may have higher heat resilience.

- Reefs that mild-severely bleached and maintained coral cover >15 % should be prioritised.
- 15-40 % coral cover: Maintain 0.04 CoTS/min.
- 40-60 % coral cover: Maintain 0.06 CoTS/min.
- >60 % coral cover: Maintain 0.08 CoTS/min.
- Can limit coral loss (but not all).

Effort Sinks

Specific to CoTS management, an Effort Sink is defined as a reef (or even site) that uses up lots of control time that cannot then be used at other reefs and detrimentally impacts the coral outcomes across the set of locations prioritised for CoTS control. Effort Sinks are emergent of the integrated management dynamics and coral-CoTS dynamics. Effort Sinks are a function of the spatial dilution of control effort, the culling thresholds targeted, and both the coral and CoTS population dynamics. In terms of resource investment, they may appear as outliers.

Implications

Inefficient distribution of resources. Locations with less coral have lower CPUE targets to offset CoTS consumption and have less coral to lose. The amount of coral saved per minute dive time (via CoTS culled) may diminish and more coral area (and larval supply) could potentially be managed by spreading cull resources. If a reef is in a very poor state, then it may be more beneficial to deploy culling efforts elsewhere based on the immediate coral that could be saved and contributing sooner to regional larval supply. The key trade-off that needs to be considered is Effort Sinks vs

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[1] Plagányi, Éva E., et al. "Multispecies fisheries management and conservation: tactical applications using models of intermediate complexity." *Fish and Fisheries* 15.1 (2014): 1-22.

CCIP-R-03: Part of the crown-of-thorns starfish innovation program resource dilution using metrics such as mean coral cover or even coral diversity.

Denuded reefs: Protect their sources

In most circumstances, CoTS threshold of 0.04-0.06 CoTS/min is appropriate even after bleaching. Culling at reefs with low coral (<5-10%) is not guaranteed to save these corals given likely slower growth rates, intensification of predation, and lag to meaningfully re-contributing to regional population dynamics (whereby climate-resilient traits could be passed on). If selecting to recover such reefs, it is suggested to maintain commitment to ongoing investment of resources into that location to keep CoTS at very low densities (<0.04 CoTS/min; *sensu* Effort Sink).

Given bleaching typically occurs late summer (after CoTS spawning), there may be little benefit to supressing reproductive output and CoTS population may naturally decline prior to subsequent summer spawning due to prey limitation (i.e. it may not be synergistic to cull to <0.04 CoTS/min). If intending to improve heat resilience, this could carry higher risks. Coral source reefs that experienced bleaching and maintained cover that supply denuded reefs may be a more reliable option to allocate control resources to.

- Reefs with <5-10 % may be hard to protect even with substantial resource investment.
- It could take years for corals to pass on favourable traits during which they're exposed to cumulative pressures (CoTS, cyclones, disease, bleaching etc).
- Identifying reefs that bleached and have >15-20% cover that supply the denuded reef for culling efforts may lead to similar outcomes and hedge culling investment to disturbance regimes.
- Maintain ~0.04 CoTS/min if decide to cull (lower could create Effort Sinks).
- Typical timing of bleaching vs CoTS spawning suggests no synergism in limiting CoTS larval supply by culling to low numbers. CoTS will likely naturally decline and/or be in poor spawning condition due to prey limitation.
- Coral cover is a relative measure and decisions between low and high coral cover reefs may need to consider coral area for inferring larval supply potential.

There are no guarantees: Hedge culling investment

Protecting heat resilient coral does not guarantee they won't be subject to other disturbances (e.g. cyclones, coral disease). This underscores the need to consider the potential for Effort Sink dynamics when selecting and allocating reefs for culling investment. Intensively focusing on fewer reefs could increase risk to control program outcomes under cumulative impacts that may otherwise be reduced via spatial dilution of effort.

- If a reef is an Effort Sink (so requires more effort to cull than expected and would appear as an outlier), it may not be feasible to control if it has bleached due to coral being in a compromised state with a concurrent CoTS population that is difficult to bring under control.

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