Tropical Water Quality Hub

National Environmental Science Programme

Technical Report

# Regional-scale modelling capability for assessing crown-of-thorns starfish control strategies on the Great Barrier Reef

Cameron S. Fletcher, Carolina Castro-Sanguino, Scott Condie, Yves-Marie Bozec, Karlo Hock, Daniel W. Gladish, Peter J. Mumby and David A. Westcott


CSIRO

# Regional-scale modelling capability for assessing crown-of-thorns starfish control strategies on the Great Barrier Reef

Cameron S. Fletcher[1], Carolina Castro-Sanguino[2], Scott Condie[3], Yves-Marie Bozec[2], Karlo Hock[2], Daniel W. Gladish[4], Peter J. Mumby[2] and David A. Westcott[1]

[1] CSIRO Land & Water
[2] Marine Spatial Ecology Lab (MSEL), University of Queensland
[3] CSIRO Oceans & Atmospheres
[4] CSIRO Data61

Australian Government

National Environmental Science Programme

Supported by the Australian Government's
National Environmental Science Program
Project 5.1 Matching the Crown-of-Thorns Starfish Integrated Pest Management to the scale of the new Control Program

National Library of Australia Cataloguing-in-Publication entry:
978-1-925514-81-0

This report should be cited as:
Fletcher C. S., Castro-Sanguino C., Condie S., Bozec Y.-M., Hock K., Gladish, D. W., Mumby P. J., and Westcott D. A. (2021) *Regional-scale modelling capability for assessing crown-of-thorns starfish control strategies on the Great Barrier Reef*. Reef and Rainforest Research Centre Limited, Cairns (59pp.).

Published by the Reef and Rainforest Research Centre on behalf of the Australian Government's National Environmental Science Program (NESP) Tropical Water Quality (TWQ) Hub.

The Tropical Water Quality Hub is part of the Australian Government's National Environmental Science Program and is administered by the Reef and Rainforest Research Centre Limited (RRRC). The NESP TWQ Hub addresses water quality and coastal management in the World Heritage listed Great Barrier Reef, its catchments and other tropical waters, through the generation and transfer of world-class research and shared knowledge.



Cover photographs: (front) COTS control vessels. (back) COTS control vessel dropping anchor near tourist pontoon. Images: Cameron Fletcher.

This report is available for download from the NESP Tropical Water Quality Hub website:
http://www.nesptropical.edu.au

# CONTENTS

# LIST OF TABLES



# LIST OF FIGURES

# GLOSSARY

**AMPTO** .................................... Association of Marine Park Tourism Operators
**Control Program**..................... A coordinated COTS Control Program run on the GBR
**COTS**....................................... Crown-of-thorns starfish (*Acanthaster* cf. *solaris*)
**COTS Control Centre** ............. Advanced tablet-based DSS being developed for the NESP COTS IPM Research Program
**CPUE**....................................... Catch-per-unit-effort, in COTS per minute bottom time
**Dive** ......................................... A single control dive at a Site on a Reef, typically of 40 minutes bottom time duration
**DSS**.......................................... Decision Support System
**Ecological Threshold** ............. The COTS density below which coral growth can outpace COTS damage at a Site, in this report typically expressed in units of CPUE
**Expanded Control Program**... The new Expanded Control Program run since November 2018
**GBR**......................................... Great Barrier Reef
**GBRMPA** ................................. Great Barrier Reef Marine Park Authority
**Historical Control Program**.... The Control Program delivered between 2012 – 2018
**Intensive Control**.................... Reef above the Ecological Threshold, revisited frequently for cull actions
**IPM**........................................... Integrated Pest Management
**Maintenance Mode** ................. Reef below the Ecological Threshold, revisited periodically for manta tow
**NESP** ....................................... National Environmental Science Program
**Priority Reef**............................ A Reef selected for control actions due to its high ecological and/or economic value
**Reef** ......................................... A single reef on the GBR, typically with its own unique identification code
**RRRC**....................................... Reef and Rainforest Research Centre
**Site** .......................................... A single site on a single Reef in the GBR, typically 10ha in size
**Vessel**...................................... Boat of contractor employed to undertake COTS control
**Voyage** .................................... A single Control Program voyage, typically lasting 10 days
**Voyage Plan** ........................... List of Reefs, in order, to be visited on the current Voyage

# ACKNOWLEDGEMENTS

The Association of Marine Park Tourism Operators (AMPTO), the Reef and Rainforest Research Centre (RRRC), and the Great Barrier Reef Marine Park Authority (GBRMPA) provided access to data and important contextual information about the field operations of the control program. This project is supported with funding from the Australian Government's National Environmental Science Program Tropical Water Quality Hub.


# STATEMENT OF ATTRIBUTION

This report represents a synthesis of work completed at CSIRO on the CoCoNet model, and at the University of Queensland on the ReefMod-GBR model. Both models represent long-running research programs into coral reef and COTS community dynamics, and as part of the work completed under this research program, the capabilities of both models were harmonized and extended to incorporate realistic details of the Expanded COTS Control Program that was rolled out on-water in November 2018.

Cameron Fletcher led the experimental design, synthesis, comparison and interpretation of model outputs, and used these to generate management recommendations. Carolina Castro-Sanguino contributed to the experimental design and the adaptation of various components of the ReefMod-GBR model to incorporate details of the Expanded COTS Control Program, as well as producing model runs of the regional management scenarios and providing interpretation of the ReefMod-GBR results. Scott Condie contributed to experimental design, led the adaptation of the CoCoNet model to incorporate details of the Expanded COTS Control Program, produced model runs of the regional management scenarios, and provided interpretation of the CoCoNet results. Yves-Marie Bozec led the development of ReefMod-GBR and with Karlo Hock contributed to the experimental design and the adaptation of the various components of the ReefMod-GBR model to incorporate details of the Expanded COTS Control Program. Daniel Gladish contributed empirical analysis of data from the Expanded COTS Control Program to estimate the number of person-Dives required to reduce a Site to the Ecological Threshold. Peter Mumby leads the Marine Spatial Ecology Lab that has developed ReefMod-GBR at the University of Queensland over a number of years, and contributed to the experimental design and selection of scenarios for the regional scale modelling synthesis. David Westcott leads the NESP COTS Integrated Pest Management Research Program under which this work was conducted, and contributed key experimental design throughout the regional scale modelling synthesis, as well as providing links into the rest of the Research Program.

# EXECUTIVE SUMMARY

Crown-of-thorns starfish (COTS; *Acanthaster* spp.) are a major threat to coral on the Great Barrier Reef (GBR) and across the Indo-Pacific. Of the increasing threats faced by the GBR, such as physical damage due to increased cyclone severity or bleaching due to rising ocean temperatures, COTS are the only threat amenable to immediate control. This makes understanding which strategies we can employ to reduce the impacts of COTS vitally important to fostering the overall resilience of the GBR.

The primary and only widely-applied method of COTS control on the GBR remains manual injection of individual starfish with bile salts or vinegar. This approach has been shown to generate ecologically-meaningful reductions in COTS impacts at both individual sites and, more recently, across entire reefs. However, due to its labour-intensive nature, it is infeasibly expensive to simply scale this approach up to cover every one of the more than 3800 reefs that make up the GBR.

It is therefore vitally important to decide which reefs across the GBR should be targeted for control in order to achieve the greatest impact. Making this decision strategically, however, is not simple. Unless COTS populations within a reef are quickly reduced to densities at which coral growth can outpace COTS damage, coral cover will continue to decrease despite management efforts. Moreover, through changes in larval dispersal, high density COTS aggregations removed at a reef one year will drive downstream impacts in terms of both which reefs experience COTS outbreaks and which reefs receive coral larvae to promote recovery several years later. A means of identifying effective solutions to these complexities is to leverage advanced regional scale modelling capable of tracking how management decisions made this year affect COTS and coral populations in subsequent years.

This report summarises progress towards providing just such a capability. It builds on two established coral-COTS reef community models of the GBR, CoCoNet and ReefMod-GBR, harmonising their capabilities and incorporating new detailed descriptions of management actions from the Expanded COTS Control Program to: 1) demonstrate a new regional-scale ensemble modelling capability for the Expanded COTS Control Program; and 2) make preliminary recommendations on which regional-scale management strategies are likely to most effectively reduce the proportion of reefs across the GBR experiencing COTS outbreaks. This represents important new capability that will underpin both the refinement of the Control Program for the current outbreak, and the development of a coordinated response to the next outbreak. The models were used to compare a range of different regional scale management strategies, including variations in total resourcing, spatial distribution of effort over both fixed and varying regions, and strategies that aimed to preserve resources by temporarily pausing control when COTS densities dropped.

A key outcome of this analysis is that the regional strategies currently being implemented by the Expanded COTS Control Program are likely to be generating ecologically-meaningful regional scale reductions in COTS outbreaks across a significant proportion of reefs on the GBR, and most if not all of GBRMPA's identified Priority Reefs. Other than increasing the number of vessels in the fleet, none of the alternative strategies for regional distribution of effort considered are likely to provide significant improvements during the current outbreak.

However, strategies that pause the Control Program near the end of an outbreak as average COTS densities fall lead to significantly worse performance as the next Outbreak begins.

Moreover, the model scenarios considered in this report made assumptions conservative compared to what has actually been implemented on-water since 2012, and what could be implemented if the current Control Program is maintained until the next outbreak begins. This suggests both that: 1) the current Control Program is likely to be generating greater outcomes than those reported; and 2) that our ability to reduce the regional impacts of COTS during the next outbreak will significantly exceed the outcomes presented in this report. This potential should be investigated further using the regional-scale modelling capability developed as part of this work.

# 1.0 INTRODUCTION

Crown-of-Thorns Starfish (COTS; *Acanthaster* spp.) are a major threat to coral on the Great Barrier Reef (GBR) and across the Indo-Pacific (Bruno & Selig, 2007; De'ath, Fabricius, Sweatman, & Puotinen, 2012; Pearson, 1981; Morgan S. Pratchett, Caballes, Rivera-Posada, & Sweatman, 2014; Masashi Yamaguchi, 1986). Although native to coral reefs across this region, COTS can cause disproportionate loss of hard coral cover during population irruptions or "outbreaks", where populations can increase six orders of magnitude in 1 – 2 years (Birkeland & Lucas, 1990; Morgan S. Pratchett et al., 2014). During such events, dense aggregations of COTS can strip reefs of 90% of living coral tissue (Dixon, 1996; Masashi Yamaguchi, 1986). Indeed, COTS have been identified as one of the major causes of coral loss and poor coral recovery on the GBR (Castro-Sanguino et al., 2021; Osborne, Dolman, Burgess, & Johns, 2011; Vercelloni, Caley, & Mengersen, 2017), being responsible for as much as 42% of all coral lost on the GBR between 1985 and 2012 (De'ath et al., 2012). Currently, the GBR is undergoing the fourth COTS outbreak recorded since the 1960's (Morgan S. Pratchett et al., 2014).

The GBR also faces a range of threats in addition to COTS, including cyclone damage (Gardner, Côté, Gill, Grant, & Watkinson, 2003; Morgan S. Pratchett et al., 2014) and bleaching (Claar, Szostek, McDevitt-Irwin, Schanze, & Baum, 2018; Hoegh-Guldberg, 1999; Hughes, 2003; Terry P. Hughes et al., 2018; Hughes, Kerry, & Simpson, 2018). In contrast to these other threats, however, COTS can be culled to remove them at specific locations across the GBR and provide immediate protection of coral (Westcott & Fletcher, 2018). This makes effective control of COTS a vital component of strategies aiming to protect the resilience of the GBR in the face of cumulative threats (Westcott, Fletcher, Babcock, & Plaganyi-Lloyd, 2016).

As a result, significant resources have been invested over the past fifty years in attempts to reduce outbreaking COTS densities across the GBR (Gladstone, 1993; Price, 2018; Rivera-Posada & Prattchet, 2012; Westcott et al., 2016), and more broadly across the Indo-Pacific, with at least 17 million starfish killed or removed at an estimated cost of US$15–44 million (Morgan S. Pratchett et al., 2014; Westcott et al., 2020). Most of these programs have involved the control of COTS at specific sites within individual reefs, either through lethal injection or in-situ removal of individuals (D. Johnson, Moran, & Driml, 1990; Westcott et al., 2020). Early attempts at local control showed limited success with large scale or severe COTS population outbreaks (Birkeland & Lucas, 1990; Richard Kenchington & Kelleher, 1992; Walsh & et al., 1971; L Zann & Weaver, 1988). However, more recent results from Australia's COTS Control Program have demonstrated that, by targeting the intensity and location of control actions using ecological insights, concerted efforts by a single control vessel at individual sites within reefs could reduce coral cover loss (Westcott et al., 2020). In response to successful control of COTS at specific sites, in early 2018 the Australian government provided funding to form the Expanded COTS Control Program and increase the fleet to five vessels (Price, 2018), with the goal of reducing impacts of COTS outbreaks across entire reefs. The first results of this new scaled-up program demonstrate that it is achieving these outcomes (Fletcher, Bonin, & Westcott, 2020; Westcott et al., 2020).

Despite the demonstrated success of the new Expanded COTS Control Program in reducing COTS densities and coral impacts across entire reefs with a fleet of five vessels, scaling this approach up to the GBR is a daunting prospect. The GBR consists of over 3800 reefs, and the current Control Program depends on repeated voyages to each controlled reef, with dives and manual removal implemented anywhere COTS are detected. Efficiently achieving significant COTS impact reduction at scale requires intelligent selection of the reefs where control will be implemented. Ideally, the location of management actions should be matched to the ecological processes driving the growth and spread of the pest population (Fletcher & Westcott, 2013). In the case of interacting COTS populations spread across the network of reefs on the GBR, understanding the most important locations or regions in which to invest management is a complex process, mediated by the spread of larvae on ocean currents, and local population dynamics on each reef.

The solution, which we investigate in this report, is to leverage advanced coral reef community models incorporating both key ecological processes and management actions. We employ two established coral-COTS reef community simulation models of the GBR, CoCoNet (Condie et al., in review; Condie, Plagányi, Morello, Hock, & Beeden, 2018), and ReefMod-GBR (Bozec et al., 2020; Bozec & Mumby, 2019). As part of this work, both models were extended to incorporate detailed descriptions of the ecological approach of on-water management decision-making in the new Expanded COTS Control Program (Fletcher et al., 2020). The two models were then used to assess the relative benefits of a range of nine alternative regional management strategies against each other, and a baseline simulation of no management.

The goals of this report are to: 1) detail the development of a regional modelling capability to underpin further refinement of the Expanded COTS Control Program; 2) assess the relative performance of the nine regional management strategies modelled; and 3) synthesise results across the two model frameworks and nine management strategies to provide a series of regional-scale management recommendations for the immediate-, short- and medium-term. The report begins by providing important background information into COTS biology, the ecological underpinning of the current Expanded COTS Control Program, and the key management decision processes on which it is based. The implementation of management components into the two GBR-scale coral-COTS reef community model systems is detailed, along with the baseline and nine management scenarios tested, and the metrics used to estimate the benefits of regional scale COTS control under different scenarios. Results are presented for each cluster of scenarios within each model. The discussion synthesises results across scenarios and models to draw out key messages, and commonalities and differences between the two modelling approaches. The conclusion summarises progress against the three aims of the report and presents three management recommendations for regional-scale COTS Control over the immediate-, short- and medium-terms.

## 1.1 COTS Outbreaks and Ecology

### *1.1.1 COTS outbreaks*

COTS are native to coral reefs across the Indo-Pacific, and at background densities of 0.1 $ha^{-1}$ cause little impact on coral reef ecosystems. During outbreaks, however, densities can increase rapidly, and the resulting populations can cause significant damage. According to Pratchett *et al.* (2014), “the first well-documented outbreaks occurred in southern Japan in the late 1950s (Yamazato 1969 in Masashi Yamaguchi, 1986) and on Australia’s Great Barrier

Reef (GBR) in the early 1960s (Pearson & Endean, 1969)", although there are several earlier reports of high densities of *Acanthaster* spp. (Dana, 1970; Vine, 1973). Although many marine organisms exhibit variability in adult abundance (Roughgarden, Gaines, & Possingham, 1988), the rate and magnitude of COTS outbreak dynamics are exceptional, with increasing abundance by up to six orders of magnitude in two years (Birkeland & Lucas, 1990; Morgan S. Pratchett et al., 2014). On the GBR, there have been four recorded outbreaks, first reported in 1962, 1979, 1993 and 2010 respectively (Morgan S. Pratchett et al., 2014).

It is unclear exactly what causes COTS populations to outbreak. Environmental conditions, such as elevated phytoplankton concentrations and low current velocities, potentially combined with a lack of predators, are thought to contribute to the initiation of COTS outbreaks (e.g. K. E. Fabricius, Okaji, & De'ath, 2010; Sweatman, 2008; Wooldridge & Brodie, 2015). However, the relative contribution of each of these drivers to the dynamics of COTS is still debated (R. C. Babcock, Milton, & Pratchett, 2016; Morgan S. Pratchett, Caballes, et al., 2017). Despite this uncertainty about the fundamental drivers of COTS outbreaks, it has been possible to develop regional scale models of coral communities and COTS populations incorporating those components of individual COTS biology that are well understood, and matching population-level dynamics to empirically observed dynamics (Bozec et al., 2020; Condie et al., 2018).

On the GBR, COTS outbreaks have consistently exhibited distinctive large-scale dynamics, driven by the dispersal of larvae on prevailing ocean currents. Primary outbreaks begin in a region referred to as the 'initiation box' between Lizard Island (14.6°S) and Cairns (17°S) (Morgan S. Pratchett et al., 2014). Larval dispersal from these reefs drives secondary outbreaks on reefs to the south of the initiation box, which in turn spread to reefs progressively further south as the outbreak propagates at a rate of around 1° of latitude every 3 years (R. Kenchington, 1977; Reichelt, Bradbury, & Moran, 1990).

Reefs experiencing outbreaks typically experience severe loss of coral, with dense aggregations of COTS sometimes consuming more than 90% of the living coral tissue (Dixon, 1996). Once coral cover is depleted, COTS populations collapse, although the specific mechanisms are not yet well understood. At a regional scale, this combination of population dynamics leads to an outbreak "front" roughly 1 – 2° degrees of latitude wide, that moves southwards along the GBR following the establishment of a primary outbreak. Within this outbreak front, a significant proportion of individual reefs, but not all, will typically experience intense COTS outbreaks and significant loss of coral cover.

Both the CoCoNet and ReefMod-GBR models are capable of reproducing key components of these COTS outbreak dynamics over the regional scales relevant to this report, up to the scale of the GBR. This includes the initiation of the current outbreak north of Cairns in 2010, the spread of the outbreak front southwards at a rate of around 1° of latitude every 3 years, the breadth of the outbreak front at any point in time of approximately 1 – 2° of latitude, and the outbreak status of individual reefs within this outbreak front. Individual reefs experience COTS outbreaks based on their local coral conditions, and the COTS larvae they receive from other outbreaking reefs, eventually followed by population collapse as coral prey is depleted.

### *1.1.2 COTS Biology*

There has been considerable research on the biology of *Acanthaster* spp in terms of reproductive biology, diet and behaviour (see Morgan S. Pratchett et al., 2014 review), but key aspects of their life cycle are still poorly known. Recent studies have shown juveniles are capable of delaying growth in the absence of coral suggesting that herbivorous juveniles can accumulate in the reef matrix for at least 6 years until favourable conditions arise (Deaker et al., 2020). The high plasticity of COTS juveniles and variability in their demographics likely contributes to their boom-bust dynamics (Deaker et al., 2020; Uthicke, Schaffelke, & Byrne, 2009), and poses many challenges for modelling their dynamics.

*Acanthaster* spp is highly fecund and fecundity increases disproportionately with increasing size (Kettle & Lucas, 1987). Large females (~40 cm diameter) can produce up to 65 million eggs per spawning event (Birkeland & Lucas, 1990; Pearson & Endean, 1969). To effectively reproduce, males and females need to be in close proximity and spawn simultaneously (R. C. Babcock & Mundy, 1992; R. C. Babcock, Mundy, & Whitehead, 1994). Consequently, reproductive success may be greatly constrained when there is a highly biased sex ratio or when population densities are low and the distance between individuals is large (see Morgan S. Pratchett et al., 2014 review and references within). Spawning is highly seasonal and driven mainly by temperature (Morgan S. Pratchett et al., 2014). In most locations, *Acanthaster* spp spawns during summer (e.g., R. Babcock & Mundy, 1993; R. C. Babcock & Mundy, 1992) and while there is evidence of multiple spawning events per year (e.g., Conand, 1983) evidence from the GBR suggest that these events usually occur only once per year, sometime between December and February (R. C. Babcock & Mundy, 1992; Morgan S. Pratchett et al., 2014).

COTS larvae are dispersed from source populations on individual reefs and are transported downstream on prevailing ocean currents (Brodie, Fabricius, De'ath, & Okaji, 2005; Hock, Wolff, Condie, Anthony, & Mumby, 2014). The larval settlement competence period begins around 11 days after fertilisation (Brodie et al., 2005), and larvae can survive in the water column for a range of durations (9 – 42 days) before settling (e.g. Olson, 1987). Many factors influence the successful dispersal of larvae, including the size and health of the source population, the competency period and dispersal duration for individual larvae, the distribution of suitable downstream habitat and the details of prevailing ocean currents in both the specific location and at the specific time of dispersal (Treml, Halpin, Urban, & Pratson, 2008).

During their larval stage, *Acanthaster* spp feed mainly on phytoplankton (K. E. Fabricius et al., 2010; J. K. Keesing et al., 1996; J. S. Lucas, 1982). It has been suggested that on the GBR larvae are severely food limited except during major phytoplankton blooms ('larval starvation hypothesis'; J. S. Lucas, 1982), when COTS larval survival increases approximately 8-fold with each doubling of chlorophyll concentration, up to 3.0 $\mu g\ l^{-1}$ (K. E. Fabricius et al., 2010). However, recent experimental studies show that developmental success to the juvenile stage occurs across an order of magnitude of chlorophyll-a concentrations (0.5–5.0 $\mu g$ chl-a $l^{-1}$), suggesting that opportunistic COTS larvae may be more resilient to low food levels than previously thought, and that eutrophic conditions may not be required for the initiation of population outbreaks (Wolfe, Graba-Landry, Dworjanyn, & Byrne, 2017).

Newly settled *Acanthaster* spp feed almost exclusively on coralline algae (J. S. Lucas, 1984; Masashi Yamaguchi, 1973; L Zann & Weaver, 1988). Consequently, high rates of settlement are found on dead substrates or rubble encrusted with coralline algae (C. R. Johnson, Sutton, Olson, & Giddins, 1991). Post- settlement mortality rates are high (J. Keesing & Halford, 1992) and transition to the juvenile stage occurs after 3 weeks of settlement when the starfish starts developing arms (Birkeland & Lucas, 1990; J.S. Lucas, 1975). While feeding on coralline algae, growth rates are slow (1.5-2.6 mm/month), but increase rapidly with the switch to feeding on corals (16.7-25 mm/month (Birkeland & Lucas, 1990; M. Yamaguchi, 1974; L. Zann, Brodie, Berryman, & Naqasima, 1987). Evidence from several studies suggests that *Acropora* and *Montipora* are the preferred coral prey for *Acanthaster* spp. (Morgan S. Pratchett et al., 2014).

Starfish juveniles are extremely vulnerable to predation (J. Keesing & Halford, 1992) which may explain their cryptic and nocturnal behavior (Morgan S. Pratchett et al., 2014). It has been suggested that Marine Protected Areas reduce the occurrence of outbreaks by supporting more diverse communities (Mellin, Aaron MacNeil, Cheal, Emslie, & Julian Caley, 2016), which contain a wider range of predators (Kroon et al. 2020), which have, in turn, been shown to reduce COTS (Cowan, Dworjanyn, Caballes, & Pratchett, 2016; Cowan, Pratchett, Messmer, & Ling, 2017; Vanhatalo, Hosack, & Sweatman, 2017).

As individuals exceed 15cm diameter and their feeding rates increase, adults become more active during daylight hours (Morgan S. Pratchett et al., 2014; L. Zann et al., 1987). Adult growth and longevity vary depending on local environmental conditions such as food availability, temperature and wave exposure (R. Kenchington, 1977; J. S. Lucas, 1984; Ormond & Campbell, 1971). On the GBR, there are records of adults up to 750 mm in diameter (Stump, 1996), and evidence of individuals living for more than 8 years (Pan, Hilomen, & Palomares, 2010).

Adults can move at an average maximum velocity of 33.3 cm $min^{-1}$ on sand (Pearson & Endean, 1969) and at much lower rates on other reef substrates (Moran, 1986). However, it is possible that different movement rates on different substrates may reflect differential motivations for movement, rather than physiological capabilities (Morgan S. Pratchett, Cowan, et al., 2017). In the absence of prey, COTS spend more time moving (cf. feeding) (De'ath & Moran, 1998) and evidence suggests that starvation can initiate movement (Sigl, Steibl, & Laforsch, 2016). Over periods of days to weeks, adults move at a maximum average rate of only 2.50–5.75 cm/min (Moran, 1986).

Both the CoCoNet and ReefMod-GBR models describe the key biological relationships between COTS and coral communities across the GBR that are important to a regional scale description of population dynamics, including predator-prey relationships between coral and COTS, natural mortality processes and disturbances due to cyclones and bleaching, and dispersal of larvae on ocean currents between reefs across the GBR. Despite the models implementing COTS population processes in fundamentally different ways, both reproduce the broad scale dynamics and periodicity of GBR-scale outbreaks. At the scale of individual reefs, both models capture juvenile mortality processes, age-stage growth of COTS populations on the reef, consumption of preferred coral food sources proportional to the size of the COTS population on the reef, and reproductive output proportional to the size of the COTS population on the reef. In addition, CoCoNet describes the ability of juveniles to delay growth in the absence of coral prey and the impact of cyclonic flood plumes on coral and COTS larvae, while ReefMod-GBR incorporates the impacts of water quality on COTS larval survival.

## 1.2 COTS Control

### *1.2.1 Background*

Prior to 2012, control efforts during COTS outbreaks on the GBR tended to be isolated and localised, and primarily focussed on removing or killing starfish (e.g. Barnes, 1966; Raymond, 1986). Those few examples where control was effective tended to be small in spatial scale (Birkeland & Lucas, 1990; Moran, Bradbury, & Reichelt, 1988). In response to the COTS outbreak that started on the GBR in 2010, a larger control program was introduced, initially to protect sites at important tourism reefs around Cairns, and then expanded to protect ecologically important sites. Between 2012 and 2018, the control program operated either one or two vessels, depending on funding availability, and the control sites visited at each reef invariably represented a small proportion of the total area of reef (Firth & McKenzie, 2015).

The data from the first five years of this program provided evidence that concerted control efforts at the scale of a site within a reef could protect coral cover from the impacts of COTS (Westcott & Fletcher, 2018; Westcott et al., 2020). In a collaboration between researchers and on-water operators, it also allowed the first implementation of ecological management principles to refine control efforts (R Babcock et al., 2014; Fletcher & Westcott, 2016). As a result of the demonstrated success of the program, in early 2018 the Australian government increased funding to create the Expanded COTS Control Program, with a fleet of five vessels (Price, 2018). The new Expanded Control Program was designed from the ground up to implement ecological approaches to management (Fletcher et al., 2020), and rolled out on water in November 2018 (GBRMPA, 2020). As part of the work presented in this report, the management processes on which the Expanded COTS Control Program is based were incorporated into the coral-COTS reef community models CoCoNet and ReefMod-GBR.

### *1.2.2 On-water control: the decision tree process*

The Expanded COTS Control Program is based around a series of ecologically-informed principles, namely: 1) effort is focused on ecologically or economically important Priority Reefs; 2) any individual Reef that is managed is managed in its entirety; 3) once control is started at a Reef, it continues until COTS have been reduced to the Ecological Threshold density at which coral growth can outpace COTS damage; and 4) only then are those Control Program resources (vessels, divers) redirected to another Priority Reef. Periodic manta tow surveillance is used to structure control actions during intensive culling at a Reef and, once COTS density at the Reef is reduced to the Ecological Threshold, to ensure that density is maintained.

In practice, these ecological principles have been implemented as a decision-tree that structures on-water decision making (Figure 1; Fletcher et al., 2020). The decision tree in Figure 1 is designed to ensure that on-water decisions are: 1) consistent with ecological principles, in that Reefs are managed as-a-whole and COTS densities are reduced to meaningful Ecological Thresholds; 2) efficient, in that the Sites at a reef with the highest density aggregations of COTS are managed first to protect the greatest amount of coral; and 3) rigorous, in that COTS densities are monitored over time and this information is used to update control tactics.

The COTS control workflow is roughly:

1) A list of Priority Reefs where control actions will be focused within each region of the GBR is provided by GBRMPA to on-water operators (see Section 1.2.2 below).
2) During a cull Voyage, a Control Program Vessel may visit a mix of new Reefs not previously controlled, Intensive Control Reefs at which culling has been conducted, and previously controlled Maintenance Mode Reefs requiring periodic re-surveillance to confirm COTS densities remain below the Ecological Threshold.
3) On arrival at Reefs not previously controlled, Maintenance Mode Reefs requiring periodic re-surveillance, and Intensive Control Reefs that have not been manta towed for 42 days or longer, control operators Manta Tow the entirety of the Reef circumference.
4) If COTS are detected during any manta tow on the entire Reef, or the most recent previous cull efforts at a Site returned CPUEs above the Ecological Threshold, then any Site at which COTS were detected is targeted for cull diving. The highest density Sites are culled first, with crews performing as many Dives as necessary to inject every COTS discovered during a comprehensive survey of the Site. As each Site is completed, dive crews are redirected to the Site on the Reef with the next highest manta tow COTS detections.
5) Divers continue culling at all Sites on a Reef at which COTS were detected during the manta tow until either every such Site has been culled, in which case the Vessel moves to the next Priority Reef, or until it is time to return to port. If all Sites on a Reef at which COTS were detected during the manta tow are culled and achieve CPUEs less than the Ecological Threshold, the Reef is moved from Intensive Control to Maintenance Mode, otherwise it remains in Intensive Control mode.

The most important components of this workflow were implemented in the CoCoNet and ReefMod-GBR regional scale models, as described in detail in Section 2.2. Specifically: 1) Vessels preferentially targeted GBRMPA Priority Reefs; 2) Vessels invested sufficient Dives at any Reef managed to reduce COTS densities to the Ecological Threshold at every Site on the Reef; and 3) Vessels only managed the number of Reefs in a year that allowed them to achieve points one and two. The models accounted for the additional effort required to control large Reefs, and the additional effort required to control Sites containing high density COTS aggregations down to the Ecological Threshold. The effort required to reduce each Site to the Ecological Threshold was estimated empirical from Control Program data, as described in Section 2.2.1.

The models reproduced an outbreak beginning in 2010 and implemented management beginning in 2019. This is consistent with the start of the new Expanded COTS Control Program but omits the previous component of the Control Program that ran from 2012 – 2018. As such, the results will reflect the potential impact of the new Expanded COTS Control Program starting, as it did, more than halfway through an outbreak, but will underestimate both: 1) the benefit had the new Expanded COTS Control Program been applied since the start of the current outbreak; and 2) the total benefit of all control actions that have actually been applied during the current outbreak.

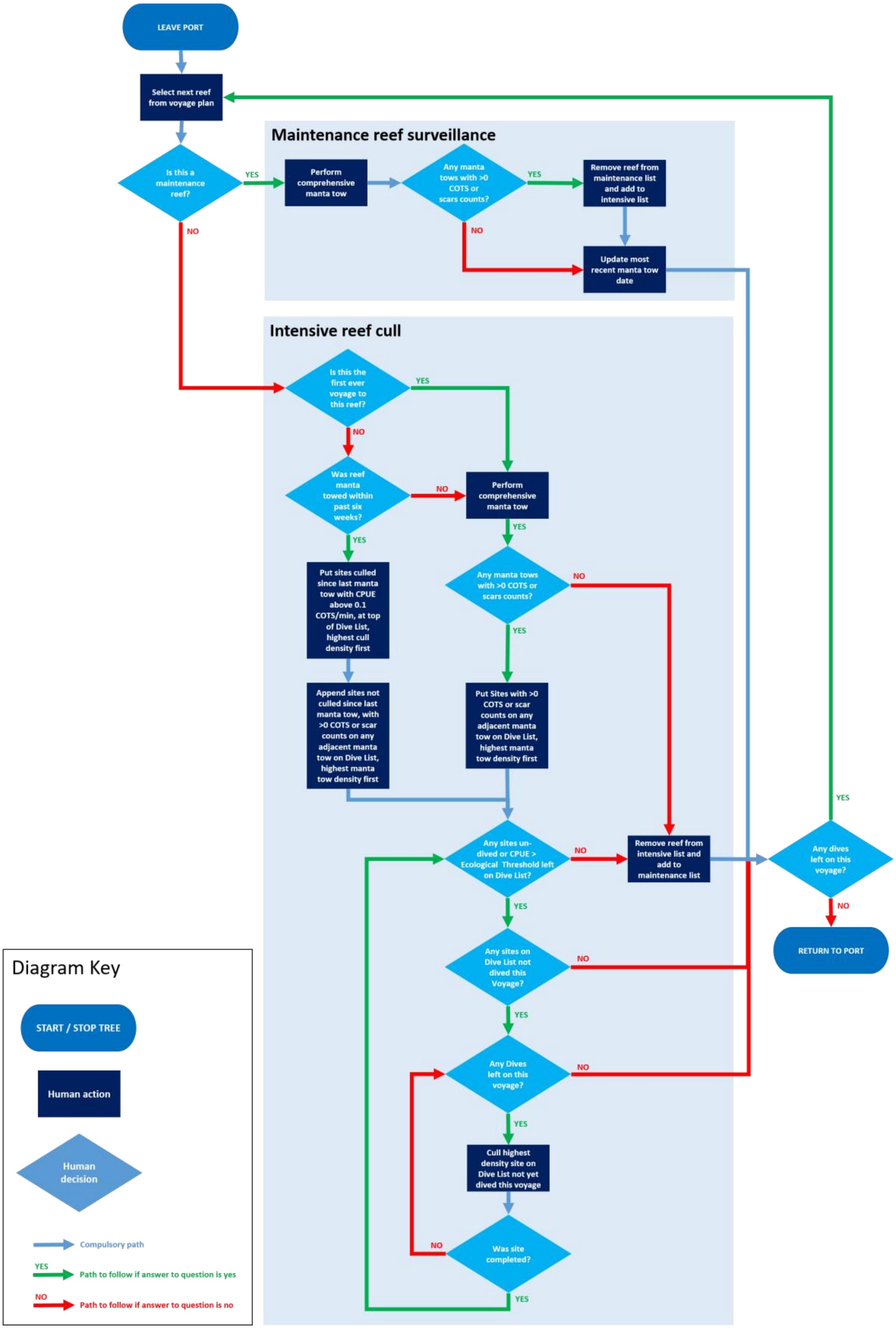


**Figure 1: The simplified on-water decision tree**

### *1.2.3 Priority Reefs*

For the purposes of operational COTS control planning, GBRMPA divides the GBR Marine Park into five Operational Regions (GBRMPA, 2020). Within each Operational Region, GBRMPA run an expert-informed process to identify a list of priority Reefs on which to focus control actions. The prioritisation process aims to identify a subset of reefs with high ecological and/or economic values, based on information including:

1) Monitoring data on COTS outbreak status of reefs across a region (where available).
2) Monitoring data on coral cover status of reefs across a region (where available).
3) Tourism visitation data that identifies reefs of high value for sustaining Reef-based industries.
4) Modelling predictions that identify reefs with high capacity to enhance reef resilience by spreading coral larvae to many other reefs.
5) Modelling predictions that identify reefs with high capacity to threaten reef resilience by receiving and/or spreading COTS larvae to many other reefs.
6) Logistical and operational knowledge that identifies reefs that are unlikely to be suitable for pest management due to their depth and/or exposure profiles.

The Priority Lists are updated prior to the beginning of each financial year using the most recent information available in each category. Each vessel within each region is then provided a list of Priority Reefs on which to focus their control actions over the coming year, along with associated information such as predefined control Sites at each Priority Reef. With few exceptions, control operators are expected to focus all control efforts on Priority Reefs.

The regional Priority Reef lists are informed by some of the same regional COTS and coral population processes described in CoCoNet and ReefMod-GBR, including modelling predictions related to the spread of COTS and coral larvae (Hock, Doropoulos, Gorton, Condie, & Mumby, 2019; Hock et al., 2017). In the Priority Lists, a yearly snapshot of the estimated larval connectivity network is combined with estimates of non-ecological measures of reef importance and operational constraints. The CoCoNet and ReefMod-GBR regional scale models, in contrast, employ a more advanced approach that represents both larval dispersal networks and source populations of COTS and corals, and accumulates population dynamics under different management scenarios over periods of years to decades, to assess alternative regional scale management scenarios. In future, the advanced regional scale modelling capability developed in this report will be extended to create a system that can provide annual recommendations on priority reefs within each Operational Region.

For the analysis conducted in this report, the details of this regional prioritisation process were captured in the CoCoNet and ReefMod-GBR regional scale modelling frameworks through incorporation of the latest priority lists available at the time of model compilation (from June 2019). Within the models, as the Sites at each Priority Reef were controlled down to the Ecological Threshold and the Reefs moved from Intensive to Maintenance Mode, the regional scale models moved control activities first to the other Reefs on the Priority List, then to other Reefs within the same Operational Region at random.

# 2.0 METHODS

The NESP COTS Regional Scale Modelling work aimed to build on two existing advanced coral-COTS community models, CoCoNet (Condie et al., in review; Condie et al., 2018), and ReefMod-GBR (Bozec et al., 2020; Bozec & Mumby, 2019). Both models have been widely tested and used on the GBR. The goal of this work was to incorporate descriptions of the management processes implemented in the Expanded COTS Control Program, and to assess the performance of a range of alternative regional strategies on outbreak dynamics.

Both models were extended to incorporate detailed descriptions of the ecologically-informed framework for on-water management decision-making in the new Expanded COTS Control Program, as described in Section 1.2.1 above and Fletcher et al. (2020). Additionally, both models implemented current regional distributions of management effort as reflected in the regional reef priority lists used in the current Control Program, as described in Section 1.2.2. The amount of control effort required to reduce COTS densities to target values at control Sites was parameterised empirically from field data from the Expanded COTS Control Program.

The two simulation models were then used to assess the relative benefits of a range of nine alternative regional management strategies against a baseline scenario incorporating no management actions. The simulated scenarios covered four key categories: 1) variations in total resourcing; 2) variations in spatial distribution of effort by Operational Region; 3) a spatio-temporal strategy focussed on the outbreak front; and 4) variation in the distribution of effort over time triggered by COTS densities across the GBR or at individual reefs.

Finally, the benefits of different strategies were calculated by running multiple iterations of each model and comparing the result to the counterfactual baseline scenario that omitted control actions entirely. Both the proportion of Reefs at which COTS outbreaks were avoided, and the total area of coral cover protected by control actions was tracked across the entire GBR. In addition, the proportion of GBRMPA Priority Reefs at which outbreaks were avoided, and the coral cover increase at controlled reefs was tracked.

In all cases, the performance of each strategy was compared to the counterfactual (no control), and to other strategies within each model framework. Direct comparisons of absolute estimates of coral cover between the two models were not possible due to different baseline predictions produced by each model even in the absence of control. These differences are not unique to the way the models describe COTS or COTS management; they have been identified in their use elsewhere on the GBR, and are considered further in the Discussion. Instead, relative performance of scenarios within each model were compared. This ensemble approach provides confidence in the outcomes generated, irrespective of variability between the models, and within each model run.

## 2.1 Reef community models

### *2.1.1 CoCoNet*

The Coral Community Network (CoCoNet) model is a spatially explicit reef meta-community model representing 3753 reefs across the GBR. It estimates changes in coral and COTS populations exposed to tropical cyclones, flood plumes, and marine heat waves (Condie et al., in review; Condie et al., 2018). Each reef is resolved at the scale of individual control sites corresponding to approximately 14 ha of available coral habitat (Westcott et al., 2020). Coral communities consist of five coral groups whose species are relatively abundant on the GBR. These groups nominally correspond to staghorn *Acropora*, tabular *Acropora*, *Montipora*, *Poritidae* and *Favids*, distinguished within the model in terms of their growth rates and susceptibility to environmental impacts and predation by COTS (Condie et al., in review).

COTS populations were size-structured, differentiating larvae, juveniles (primarily herbivorous) and four corallivorous adult classes. Size classes equated with age (increasing one age-class each year) except that juveniles delayed maturing to adults if the availability of their preferred coral prey groups was low (Deaker et al., 2020), and size plateaued after 4-years as an adult. COTS had a preference for faster-growing corals (Morello et al., 2014; M. S. Pratchett, 2010) and populations declined when these became rare. Predator-prey cycles between COTS and coral produced regular outbreak cycles in CoCoNet (Condie et al., 2018). However, to ensure that the phase of these outbreaks aligned with observations, one year before the initiation of each outbreak COTS densities were halved across all GBR reefs except those within the initiation box. The same procedure was applied in 2025 to ensure that the projection period broadly followed the historical outbreak pattern.

Reef connectivity was determined by spawning, larval transport by ocean currents, and settlement onto neighbouring reefs. Full details of how this was implemented are available in Hock et al. (2014). For all coral groups, larval production was proportional to their area coverage, whereas COTS larval production was proportional to the number of adult starfish, increasing by a factor of 4 with each of the first 3 adult size-classes before plateauing (R Babcock et al., 2014; Morgan S. Pratchett et al., 2014). The probability of successful recruitment onto a reef from spawning on an upstream reef was proportional to the connectivity estimated from particle tracking model results (Hock et al., 2019; Hock et al., 2016; Hock et al., 2014; Hock et al., 2017), although recruitment was reduced by coral rubble previously generated by cyclone and bleaching-induced coral mortality. The particle tracking model used ocean currents from the eReefs 1-km resolution hydrodynamic model (Condie et al., in review; Steven et al., 2019).

Reefs were subjected to environmental stressors in the form of tropical cyclones and flood plumes and heat waves. These stressors changed over the simulations according to historical data prior to 2020, and then according to statistical climate projections (RCP 2.6). Tropical cyclone events were applied stochastically at frequencies and intensities consistent with recent historical conditions (Puotinen, Maynard, Beeden, Radford, & Williams, 2016; Nicholas H Wolff et al., 2016). Coral mortalities within the spatial footprint of different cyclone intensities (categories 1-5) were parameterized using results from post-cyclone surveys (Condie et al., 2018; Katharina E. Fabricius et al., 2008), with commensurate increases in coral rubble cover. Faster-growing coral groups (staghorn *Acropora* and tabular *Acropora*) were more susceptible to cyclone damage than slower-growing groups (Faviidae and Poritidae; Katharina E. Fabricius et al., 2008). Cyclone-induced flood plumes reduced coral growth rates and increased rates of COTS recruitment over a zone that expanded further offshore with increasing cyclone category (Nicholas H. Wolff, Mumby, Devlin, & Anthony, 2018). It was assumed that the frequency distribution for future cyclones is similar to the past two decades.

Marine heatwaves were implemented as random events dependent on the cumulative exposure of reefs to high temperatures expressed in terms of degree heating weeks (DHW). Coral bleaching mortality within the spatial footprint of marine heatwaves varied stochastically, with the average increasing with DHW (Terry P. Hughes et al., 2018). Prior to 2020, heat waves followed observed patterns, after which plausible future scenarios for maximum annual DHW were described by a sigmoid curve with parameters estimated from past sea surface temperature distributions (Nicholas H. Wolff et al., 2018) and extrapolation of past bleaching events (Lough, Anderson, & Hughes, 2018). The average proportion of locations bleached on the GBR per annum were aligned with empirical estimates from the Australasian region (Terry P. Hughes et al., 2018). The thermal tolerance of faster-growing coral groups was assumed to be lower than slow-growing groups (Marshall & Baird, 2000).

Each simulation started in 1950 and ended in 2030, with the first 35 years treated as an equilibration period. Because the model and model forcing included a large number of stochastic elements, every run was repeated 50-times allowing ensemble statistics to be calculated (i.e. 50-member ensembles). Ensemble means and variances were found to be insensitive to ensemble size for more than 25 members (Condie et al., in review).

Alternative COTS control strategies were tested by comparing their performance with a baseline scenario involving no COTS control. The control strategies tested in this study are defined in Table 1.

Rate parameters such as growth, predation and natural mortalities have been calibrated for coral and COTS population dynamics at the scale of individual reefs (Morello et al., 2014; Plaganyi et al., 2014) and smaller networks of reefs (Condie et al., 2018). Connectivity and associated larval recruitment parameters were calibrated for the GBR using LTMP data (Condie et al., in review). Here we present comparisons with data from the LTMP for coral cover, and COTS outbreaks (Figure 2).

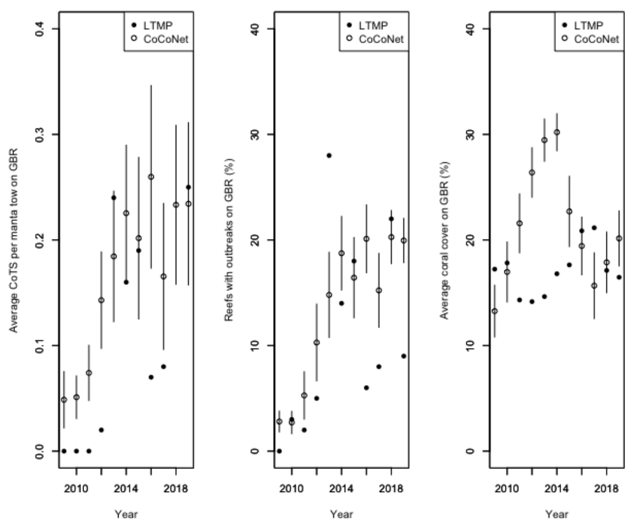


**Figure 2: CoCoNet time-series comparing model ensemble results (circles) with LTMP data (red lines) averaged over GBR reefs: fractional coral cover (top); COTS density in COTS per manta tow (centre); and fraction of reefs with active COTS outbreaks (> 1.0 COTS per manta)**

### *2.1.2 ReefMod-GBR*

ReefMod-GBR is a spatially-explicit model of coral and COTS populations that integrates the effect of larval dispersal, water quality, cyclones and bleaching across 3,806 reefs of the Great Barrier Reef (Bozec et al., 2020; Bozec & Mumby, 2019). With a six-month time-step, the model tracks the size of individual coral colonies of three groups of acroporids (arborescent, plating and corymbose) and three non-acroporid groups (pocilloporids, encrusting and massive corals) driven by demographic processes (settlement, growth, reproduction and mortality) that are characteristic of a mid-depth (~5–10 m) reef environment. Processes of coral recovery and stress-induced mortality were calibrated with regional data, leading to realistic modelling of coral population dynamics on the GBR, tested extensively against the long-term datasets of the AIMS LTMP (Bozec et al., 2020).

Outbreak dynamics of COTS are simulated with a cohort model where starfish density is structured in 6-month age classes. COTS demographics are subject to nutrient-limited larval survivorship and age-specific mortality. The model implements the effect of chlorophyll concentrations on larval survivorship (K. E. Fabricius et al., 2010), which affects larval connectivity at local to regional scales. Mortality-at-age, fecundity and size-specific consumption of each coral type are derived from literature data.  The COTS population model was calibrated with empirical data from Lizard Island (Morgan S. Pratchett, 2005; M. S. Pratchett, 2010). Details of the calibration are provided in Bozec et al. (2020) but are briefly summarized here. COTS and coral populations were initialized with density-at-size and cover data reported in late 1996 around Lizard Island. Simulations were run by adjusting adult mortality, settlement rate and consumption on corals until a good fit was achieved between the observed and modelled trends in coral cover and COTS density (Figure 3 A and B). COTS populations were forced to collapse after 2 years as observed (Morgan S. Pratchett, 1999, 2005). With these adjustments, the model was able to reproduce the temporal changes in COTS size structure observed in the densities reported from Lizard Island (Figure 3 C and D).

With this calibration, the COTS model can reproduce the long-term dynamics of secondary outbreaks triggered by episodic events of external larval supply (Figure 4). The reproduced dynamics are consistent with the observed return time of COTS outbreaks and their impacts on coral cover.

ReefMod-GBR simulates coral and COTS demographics on individual reefs linked by larval connectivity (Hock et al., 2019; Hock et al., 2014; Hock et al., 2017) and exposed to temporally- and spatially-realistic regimes of acute stressors (cyclones and mass coral bleaching) and water quality (suspended sediments and chlorophyll concentrations) informed by the eReefs coupled hydrodynamic-biogeochemical model (Baird et al., 2017). As a result, model simulations can reconstruct recent coral trajectories that are consistent with GBR monitoring observations (~60 LTMP sites), while estimating the impacts of each stressor at reef and regional scales (Bozec et al., 2020). To reconstruct the spatial dynamics of COTS outbreaks across the GBR over the period 2008 - 2017, the model combines demographic predictions with the observed abundance of COTS at 289 reefs for which monitoring data is available. Model simulations are initialized (in winter 2007) with COTS densities predicted by the Coral Community Network (CoCoNet) model (Condie et al., 2018) run between 1985 - 2007. At the subsequent time steps, COTS densities are predicted by ReefMod-GBR except where COTS surveys were available on a given year, in which case the model predictions are replaced by observed COTS densities.

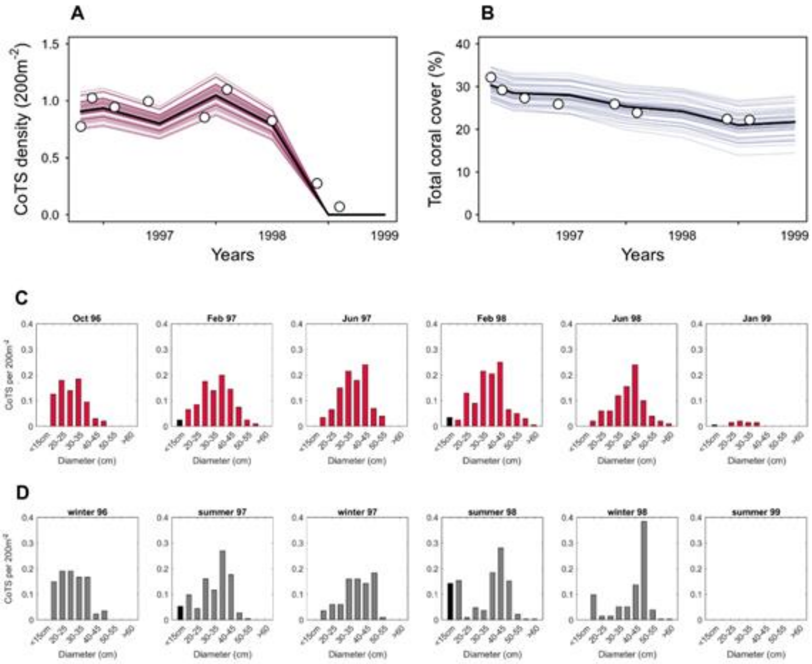


**Figure 3: Temporal changes in (A) COTS densities and (B) coral cover as observed at Lizard Island (white dots, Pratchett 2005, 2010) and as simulated by ReefMod-GBR (coloured lines: replicate trajectories; black lines: average trajectories) after calibration. (C) and (D) show the associated changes in, respectively, the observed and simulated frequency distribution of individual sizes (starfish maximum diameter). Reproduced from Bozec et al. 2020.**

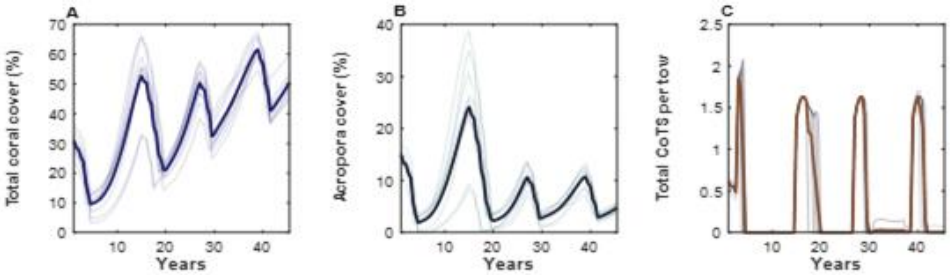


**Figure 4: ReefMod-GBR simulated changes in total coral cover (A), cover of preferred coral prey (3 acroporid groups) (B), and COTS density per tow (C) on a hypothetical reef exposed to recurrent periods of external larval supply (representative of a 12-year return time of primary outbreaks) in the absence of acute disturbances (bleaching and cyclones).**

## 2.2 Modelling the Control Program

A broad outline of the methodology followed in the new Expanded COTS Control Program is provided in Section 1.2.1 and described in detail in Fletcher *et al.* (2020). The aspects of this process most important to regional scale modelling were incorporated into both the CoCoNet and ReefMod-GBR models. Specifically, the two models described: 1) the focus of effort within certain Operational Regions; 2) within these Regions, the focus of effort on identified Priority Reefs; and 3) within these Priority Reefs, the application of a strict decision tree process designed to: a) at every Reef that was managed, reduce every Site to the Ecological Threshold at which coral growth could outpace COTS damage; and b) to only start managing additional Reefs once the current Reefs had been reduced to that Ecological Threshold.

In practice, this was implemented in the models by:

1) distributing vessels within the actual Operational Regions employed by GBRMPA;
2) using the actual Priority Reef list from 2019 for each Operational Region;
3) assigning to each Vessel a total of 5760 Person-Dives a year; and then
4a) for CoCoNet:

- i) tracking the COTS population at each ~14ha Site around a Reef,
- ii) calculating the number of Dives needed to reduce COTS to the Ecological Threshold at each Site;
- iii) reducing COTS density at each Site to the Ecological Threshold, and then
- iv) aggregating the total effort required to control the Reef

4b) for ReefMod-GBR:

- i) taking the Reef-average COTS population predicted by the model in a given year;
- ii) spreading COTS across a number of Sites related to the area of the Reef,
- iii) distributing the density of COTS at each Site based on the empirical patch distribution of COTS density observed in control program data; then
- iv) calculating the number of Dives needed to reduce COTS to the Ecological Threshold at each Site on the Reef;
- v) reducing COTS density at the Reef to the Ecological Threshold.

5) each Vessel visiting as many Reefs in its Region as possible each year.

Further specifics of the underlying models and the implementation of each step of this process is outlined in the sections below.

### *2.2.1 Empirical estimation of control effort required to achieve Ecological Threshold*

Implementing control actions within CoCoNet and ReefMod-GBR required: 1) a description of the order in which Reefs and Sites were controlled, detailed further in sections 2.2.2 and 2.2.3 below; and 2) a relationship that estimated the total amount of effort, expressed as a number of person-Dives, required to successfully control each Site and each Reef at which control was conducted.

The stated objective of both the current Control Program and the scenarios considered in this report is to reduce the density of COTS at each Site to the Ecological Threshold at which coral growth at a Reef can outpace COTS damage (Fletcher et al., 2020; Westcott et al., 2016). This Ecological Threshold has been estimated by Babcock et al. (2014) in terms of catch-per-unit-effort (CPUE), as 0.04 COTS per minute bottom time at Reefs with coral cover less than 20%.

We used data from the first seven months of the new Control Program, run using the same framework modelled in this analysis, to establish an empirical relationship between the density of COTS first detected at a Site prior to control, inferred from initial manta tows, and the total amount of effort that was then required at that Site to successfully reduce the COTS density to the Ecological Threshold. We used data from 1 November 2018 through 18 June 2019, with observations aggregated per Voyage and Site, totalling 834 observations over 31 reefs (Figure 5).

This process involved three steps: 1) using empirical data to establish a relationship between the density of COTS at a Site and the CPUE achieved when cull actions were taken there; 2) using this relationship to calculate how many COTS would be culled at a Site with a given density; and 3) combining these two steps iteratively to calculate how many times a Site must be culled to reduce from a specified starting density to the density at which cull actions achieve a CPUE of < 0.04 COTS per minute bottom time.

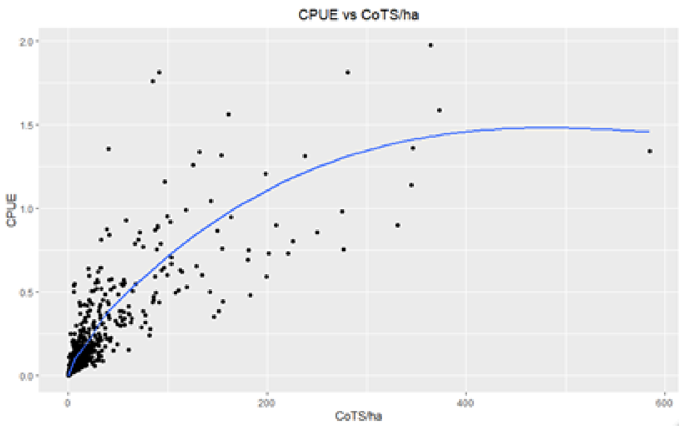


**Figure 5: Scatterplot of CPUE (y-axis) vs. COTS/ha (x-axis) of available IPM control program data from 1 November 2018 through 18 June 2019. The blue solid line highlights a general smooth trend term of CPUE against COTS/ha.**

We used random forests to model CPUE as a function of COTS/ha (Breiman, 2001). A random forest model is an ensemble machine learning-based approach that aggregates a series of decision trees, allowing estimation of a nonlinear relationship between the response and covariates nonparametrically. We used the "randomForest" package (Liaw & Wiener, 2002) in the R statistical programming language (R Core Team, 2020). A random forest built with COTS density and Site area as covariates produced a model explaining 71.21% of the total variation of CPUE. The model was validated by 10-fold cross validation.

The amount of effort required to reduce a Site to the Ecological Threshold was estimated iteratively. An algorithm was constructed to predict CPUE for a given density and area, then calculate a new density. The process was repeated until the associated CPUE was below the set Ecological Threshold. Formally, for a specific site $l$ and time $t$:

- $d_{lt}$ was the density (COTS/ha),
- $a_l$ was the area of the site (in m$^2$),
- $\mathrm{CPUE}_{lt}$ was the associated CPUE,
- $e_{lt}$ was the amount of effort (dive time), and
- $c_{lt}$ was the number of COTS.

$f(\cdot)$ was the estimated random forest function predicting CPUE as a function of COTS density and area. Then, for a given density and area at site $l$ and time $t$, $\mathrm{CPUE}_{lt}$ was calculated as

$$\mathrm{CPUE}_{lt} = f(d_{lt}, a_l). \quad (1)$$

This value was then used to calculate the number of COTS left at the site at time $t + 1$ by:

$$c_{l,t+1} = c_{lt} - e_{lt}\mathrm{CPUE}_{lt}. \quad (2)$$

The resulting number of COTS, $c_{l,t+1}$, was then converted to density $d_{l,t+1}$ at time $t + 1$. This process was repeated between Equations (1) and (2) for $t = 1, \ldots, T$, where $T$ is the time at which the $\mathrm{CPUE}_{lT}$ fell below the Ecological Threshold of 0.04 COTS per minute bottom time (R Babcock et al., 2014). The total amount of effort required to reduce the COTS density of a site below the ecological threshold was defined as $E = \sum_{t=1}^{T} e_{lt}$.

This was used to create an empirical relationship for the total amount of effort needed to reduce a Site to the Ecological Threshold given a starting density using a simple linear model. Assuming a standard Dive consists of 40 minutes of bottom time, the total number of person-Dives required to reduce a Site to the Ecological Threshold was estimated as:

$$\log(E) = 5.116 + 0.665 \log(\mathrm{COTS/ha}), \quad (3)$$

where $E$ is the total amount of effort in person-Dives required to reduce the Site to the Ecological Threshold and $\log$ refers to the natural logarithm. This regression has an associated $R^2$ value of 0.863.

### *2.2.2 CoCoNet*

Implementation of COTS control in the CoCoNet followed the approach used by control vessels currently operating on the GBR (R. C. Babcock et al., 2020; Westcott et al., 2020). Control first targeted GBRMPA Priority Reefs, then moved onto other Reefs as allowed by Vessel capacity. Scenarios used either 2, 5 or 8 vessels, each carrying 8 divers. Every vessel conducted 20 voyages per year, each lasting 10-days over which 36 dive sessions were completed (i.e. average of 4 Dives per day with 1-day lost in transiting). This gave a total of 8 x 20 x 36 = 5760 individual person-Dives per Vessel per year. Each Dive took place at a single Site within a Reef, with the size of each Site equating to the area that could be covered by a single Dive by eight divers under average COTS densities (approximately 14 ha).

COTS were killed sequentially at each Site, with total effort estimated from equation 3 above, until numbers fell below the Ecological Threshold (0.04 COTS / minute bottom time CPUE, equivalent to 0.075 COTS per manta tow in the model). When reducing COTS populations to the Ecological Threshold, it was assumed that younger COTS were harder to detect, and therefore a smaller proportion of them were controlled. Hence, after culling, increasing size classes were left with average abundances of 0.63, 0.29, 0.065 and 0.015 times the threshold (MacNeil et al. 2016). The number of individual dives required to reduce COTS at a Site below the Ecological Threshold was estimated by the empirical relationship described in Section 2.21 above. Once a Site had been reduced below the Ecological Threshold, control activities moved to the next dive Site (or next Reef if all Sites at the current Reef had been treated). The total number of Sites at each Reef, and therefore also the total amount of effort to successfully control a Reef, was estimated based on the size of the Reef. This process continued until all Dives available for that year had been fully utilized. Reefs controlled in prior years continued to be monitored and retreated as required.

### *2.2.3 ReefMod*

As with CoCoNet, in ReefMod-GBR control effort was tracked at the level of individual control Sites. Where control was implemented it reduced COTS density to the Ecological Threshold, corrected by age-size class detectability (MacNeil et al., 2016). The Ecological Threshold COTS density was implemented as for CoCoNet, with a site-level Ecological Threshold of 0.075 COTS/tow, equivalent to a CPUE of 0.04 COTS/min (R Babcock et al., 2014), based on empirical data from current control program.

To implement the culling of COTS in ReefMod-GBR, each visited reef polygon (i.e. out of the 3,806 reefs, only those visited according to control strategy) was divided into a number of Sites and reef-level COTS densities were distributed across all Sites. Reef-level COTS densities in non-visited reefs remained unchanged. On visited Reefs, the number of Sites per Reef was determined based on Reef perimeter (km) following the equation: number of Sites = 1.725 x Reef perimeter (km), or around 580m per Site (Fletcher et al., 2020). Reef-level COTS abundance was then distributed across Sites based on the average within-reef distribution of COTS abundance observed by manta-tow surveys (data from Eye on the Reef and The Reef Joint Management Program). To obtain this distribution, we pooled the COTS observation data for all surveyed reefs over three consecutive manta tows assuming that three tows cover the length of a control site (~600m). We then determined the proportion of Reef-level COTS population expected to be observed at each Site by using this distribution to randomly generate a set of proportions (with a reef-level sum of 1) across the Sites on a Reef, and divided the Reef's COTS population across the Sites accordingly. After allocating COTS to individual Sites, only Sites that were found to have COTS populations above the Ecological Threshold were controlled.

After applying control to a Site, a new distribution of COTS size classes on this Site was generated to reflect the impacts of control effort based on detectability, with large size classes reduced the most based on the detectability reported in McNeil et al. (2016), while the densities of juveniles below the detection threshold remained unchanged (Bozec et al., 2020). After control was applied at each Site, the new Reef-level COTS population was calculated to reflect the impacts of density reduction on controlled Sites.

Control effort was modelled as the total number of diving hours (36 dive sessions per voyage) based on number of divers per boat (8 divers) and voyages per year (20 voyages). The effort (i.e. number of person-Dives) required to reduce COTS density to the Ecological Threshold at a Site was dependent on COTS density following the empirical analysis described in Section 2.2.1. Total yearly effort was divided by 2 (i.e. 6-month effort) in order to match ReefMod-GBR time steps. Control efforts first targeted GBRMPA Priority Reefs in a random order (from a list of Priority Reefs relevant to each regional strategy), then non-priority reefs in a random order (as relevant to each regional strategy) until all available effort for that time step had been fully allocated. If there was effort remaining after all the Priority and non-priority Reefs had been treated, the model randomly visited Reefs outside of the focal region. The decision framework leading to the deployment and processing of COTS control in a given year is explained in the flow chart below (Figure 4).

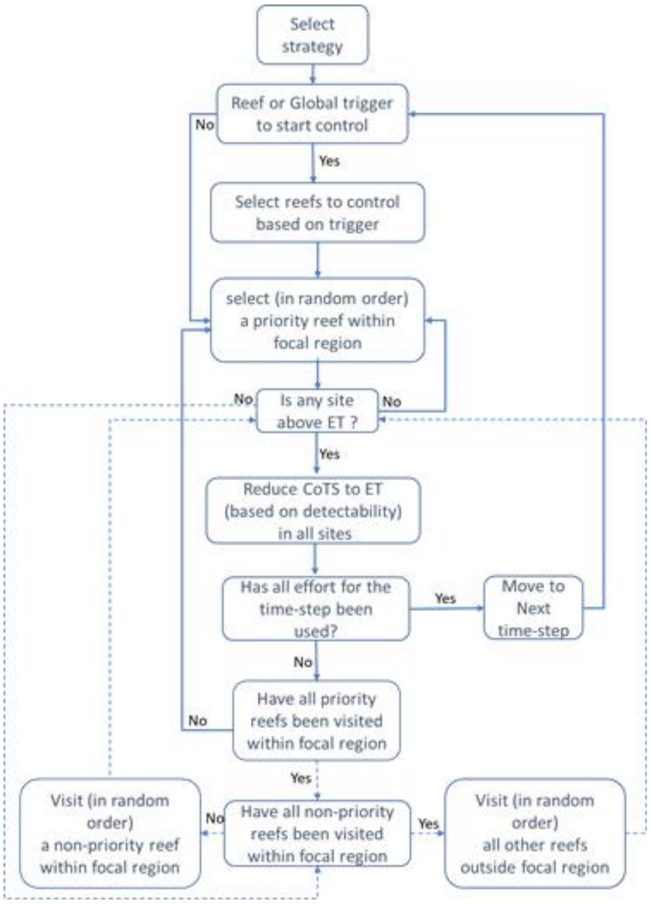


**Figure 6: Rule-based decision framework to implement COTS control strategies in ReefMod-GBR. Solid lines represent first pathway to control priority reefs. Dashed lines alternative pathway to control non-priority reefs if effort allows.**

## 2.3 Scenarios

Nine regional management scenarios across four “clusters” were considered (Table 1), designed to establish which general regional principles most effectively: 1) reduced COTS outbreaks; and 2) protected coral across the Priority Reefs and the GBR. All management scenarios were compared against the counterfactual of a tenth baseline scenario in which no management actions were implemented. The goal was to investigate sufficient scenarios to establish what makes regional strategies effective, within the constraints of the run times required to generate ensembles of model results.

The four scenario clusters examined four areas of importance to the current Expanded COTS Control Program: 1) the effect of total resourcing on Control Program impact; 2) the spatial distribution of vessels and hence Control Program effort across the GBR; 3) whether a reactive spatio-temporal strategy tracking the outbreak front could outperform strategies based on fixed regions; and finally, 4) whether strategies that change how much effort is invested through time based on COTS densities could outcompete continuously operating strategies. These clusters, and the strategies considered within them, are described in more detail below.

**Table 1: COTS control strategies run by ReefMod-GBR and CoCoNet. PR: priority sites; ET: ecological-threshold COTS density.**

| ID | Effort (No. vessels) | Focal region(s) | Global trigger to run control program | Trigger to control a reef | Trigger to control a site |
|---|---|---|---|---|---|
| 2b-GBR | 2 | Entire GBR | N/A | N/A | COTS > ET |
| 5b-GBR | 5 | Entire GBR | N/A | N/A | COTS > ET |
| 8b-GBR | 8 | Entire GBR | N/A | N/A | COTS > ET |
| 5b-NC | 5 | North & Central (10-21°S) | N/A | N/A | COTS > ET |
| 5b-C | 5 | Central (14-21°S) | N/A | N/A | COTS > ET |
| 5b-CS | 5 | Central & South (14-24°S) | N/A | N/A | COTS > ET |
| 5b-GBR-Outb | 4 in North-Central, 1 in South | ±1° latitude around outbreaking reefs | N/A | N/A | COTS > ET |
| 5b-GBR-Global | 5 | Entire GBR | 10% of PR ≥ 0.22 COTS/tow | N/A | COTS > ET |
| 5b-GBR-Reef | 5 | Entire GBR | N/A | COTS ≥ 0.22 | COTS > ET |

### *2.3.1 Baseline Scenario (no management)*

For ReefMod-GBR, all scenarios (one counterfactual with no COTS control + nine COTS control strategies) were run under the RCP2.6 climate scenario predicted by the MIROC climate model, which has been shown to project a moderate decrease in coral cover for the remainder of the 21st century (Mason, Bozec, Hock, & Mumby, 2020). For CoCoNet, each scenario was run from 1950 to 2030, with the first 35 years treated as an equilibration period. Every run was repeated 50-times allowing ensemble statistics to be calculated; ensemble means and variances were found to be insensitive to ensemble size for more than 25 members (Condie et al., in review). For ReefMod-GBR, each scenario was run from 2008 to 2050 (i.e., including the hindcast with no control) with 50 realisations (simulations) to capture the uncertainty about and variability in the frequency and magnitude of disturbance events and their effects on coral-COTS dynamics

### *2.3.2 Total amount of effort*

Three total resourcing scenarios were considered; 2, 5 and 8 vessel fleets (Scenarios 2b-GBR; 5b-GBR and 8b-GBR in Table 1, respectively). All vessels were spread across the entirety of the GBR; that is, any Vessel could control any Reef in any Operational Region.

Vessel effort was directed to Priority Reefs across the GBR first, and only when they were all successfully controlled with every Site below the Ecological Threshold, were other Reefs across the GBR selected for control randomly.

Once a Reef was selected for control, any Site at that Reef at which COTS densities were estimated to be above the Ecological Threshold was also selected for control. The total amount of person-Dives required to control each Site depended only on the COTS density at that Site (equation 3). The COTS remaining in each age-size class at each Site following control actions were then incorporated back into CoCoNet and ReefMod-GBR models, as described in Sections 2.2.2 and 2.2.3 above.

The number of Reefs controlled in a given year was determined by the amount of effort available across the fleet of 2, 5 or 8 vessels, the modelled density of COTS predicted at the Reefs selected for control, and how many of them could be completely controlled before the available effort was all used. COTS densities on Reefs successfully controlled in one year of the model gradually recovered following control, but generally required less or no control for the years following successful control, and so as control continued progressively more Reefs were controlled to the Ecological Threshold.

### *2.3.3 Fixed distribution of effort*

Three scenarios that constrained where on the GBR effort was invested were considered, based on the Operational Regions used by GBRMPA in the current Expanded COTS Control Program: the North and Central regions; the Central region only; and the Central and Southern regions (Scenarios 5b-NC; 5b-C and 5b-CS in Table 1, respectively).

All three scenarios considered only the current arrangement based on a fleet of five Control Program Vessels. In all three scenarios, at any Reef selected for control, any Sites with COTS at densities higher than Ecological Threshold had sufficient effort invested to reduce them to the Ecological Threshold.

Each Vessel operated as in the three resourcing Scenarios (2b-GBR; 5b-GBR and 8b-GBR), with the exception that only Reefs within the scenario Region or Regions could be selected for control during each year of the model. Again, Priority Reefs within the Region were selected first, and once they were successfully reduced to the Ecological Threshold, other Reefs within the Regions were selected for control randomly.

### *2.3.4 Responsive spatio-temporal distribution of effort*

One dynamic scenario that invested effort “near” the outbreak front was considered. This was implemented in the same way as the three scenarios that constrained control to fixed regions (5b-NC; 5b-C and 5b-CS), except that instead of the region from which four of the Vessels could select Reefs for control being fixed, it was defined as ± 1° of latitude from the centre of the outbreak front each year. The fifth Vessel was constrained to operate in the southern Region.

The scenario considered a fleet of five Control Program Vessels, and at any Reef selected for control, Sites with COTS above the Ecological Threshold had sufficient effort invested to reduce them to the Ecological Threshold.

The location of the outbreak front was determined by fitting a Gaussian distribution to COTS densities across the GBR against latitude at the start of each year of the model run, and setting the middle of the “outbreak front” to the mean of the Gaussian peak. As the half-width of the

Gaussian distribution was approximately 1 degree, the breadth of the management zone in this scenario was set to ± 1° of latitude of the centre to encompass the outbreak front.

At the start of each year, only Reefs within ± 1° of latitude from the position of the outbreak front could be selected for control that year by four of the fleet Vessels. Priority Reefs within this region were selected first, and once they were successfully reduced to the Ecological Threshold, other Reefs within the Regions were selected for control randomly.

### *2.3.5 Triggers to pause and restart control*

Two scenarios were used to investigate whether there are larger-scale metrics that can guide when to pause and restart control at individual Reefs or across the entire GBR without having to sample every Site at every Reef directly (Scenarios 5b-GBR-Reef 5b-GBR-Global in Table 1, respectively). The two scenarios are technically similar but motivated by different management questions.

The Reef-scale COTS density threshold investigated whether a Reef-averaged COTS density trigger of 0.22 COTS/manta tow could be used to decide whether to control a Reef or to move onto the next available Reef. If this was an effective strategy, it could reduce the time spent at Reefs that have a small number of Sites above the Ecological Threshold, but overall low Reef-average COTS densities; that is, a lot of COTS at few Sites but most Sites with few or no COTS.

The global scenario instead investigated under what conditions control across the GBR could be paused completely. This is an important scenario, because it captures the way Control Programs have run during past outbreaks. In years where the proportion of Priority Reefs exhibiting Reef-average COTS densities of 0.22 COTS/tow fell below 10%, no COTS control was implemented across the GBR. In normal circumstances, this condition could only be met: 1) if the Control Program was successful at reducing COTS densities right across the GBR; or 2) if the outbreak ends. The second of these reflects what has happened at the end of previous outbreaks, when COTS control efforts have ceased as COTS outbreaks at individual Reefs have become less prevalent. This scenario allows us to investigate the consequences of temporarily pausing COTS control when COTS densities across the GBR fall at the end of an outbreak.

Both scenarios considered a fleet of five Control Program vessels. At any Reef selected for control, any Sites with COTS at densities above the Ecological Threshold had sufficient effort invested to reduce them to the Ecological Threshold. Reefs could be selected for control from anywhere across the GBR. However, for Scenario 5b-GBR-Reef, only Reefs with > 0.22 COTS/tow were selected for control. For Scenario 5b-GBR-Global, if fewer than 10% of Priority Reefs across the GBR had COTS densities > 0.22 COTS/tow then no Reefs were selected for control, otherwise any Reef across the GBR could be selected for control. In both cases, Priority Reefs were selected for control before other Reefs.

## 2.4. Calculation of benefits

Three metrics of Control Program benefit were considered, based on the goals of the Control Program. Specifically, the proportion of Reefs at which COTS outbreaks were avoided, both

1) within the portfolio of Priority Reefs identified by GBRMPA as those at which they most want to avoid or reduce COTS impacts; and 2) across the GBR as a whole, as well as 3) the additional area of coral protected by the actions of the Control Program across the breadth of the GBR.

To ensure that the benefits of control could be distinguished from the stochastic processes driving the underlying coral/COTS community models, such as bleaching events or cyclones, each model run was compared against the counterfactual scenario involving no control for the same sequence of stochastic drivers. Benefits were calculated as the year-by-year difference between simulation outputs of the control strategy and outputs of the counterfactual (i.e. pairwise comparison of the 50 replicate simulations under each scenario).

The three metrics were calculated as follows: proportional reduction in total number of outbreaking reefs (i.e. with reef-level COTS density ≥ 0.22 individuals per tow) compared to the counterfactual 1) within the portfolio of Priority Reefs; and 2) across the entire GBR; and 3) total coral cover area ($km^2$) gained (compared to counterfactual), calculated as the cumulative sum of % coral cover × reef area ($km^2$) across the entire GBR (i.e. summed over all GBR reefs).

Because the effect of future climate on corals is uncertain (Mason et al. 2020), the evaluation of control benefits was performed only over the first 12-years of control implementation (i.e. 2019-2030).

# 3.0 RESULTS

Both regional model systems, CoCoNet and ReefMod-GBR, simulated the nine scenarios outlined in Section 2.3 across ensembles of 50 model runs, compared each of those model runs against the baseline counterfactual scenario containing the same stochastic processes but no control, and then produced results against the three benefit metrics described in Section 2.4. CoCoNet produced results as plots illustrating the mean and standard error each year from the stochastic runs, while the ReefMod-GBR smoothed trend plots show the mean and 95% confidence intervals.

ReefMod-GBR model simulations revealed important variations in the magnitude of benefits of COTS control in terms of the number of outbreaking reefs and total coral cover area. Overall, GBR-wide benefits of COTS control increased over time from the first year of implementation (i.e. 2020). Within the GBRMPA Priority Reefs, many regional strategies were able to avoid outbreaks completely by 2028, with more effective strategies reaching this point sooner. Across the GBR, the number of outbreaking reefs declined over time, with most strategies achieving the maximum benefits at the end of the decade. Maximum gains in total coral cover area were achieved in 7 years, after which coral cover benefits slightly declined and then stabilised (i.e. stop declining). The decline in benefits from 2026 is likely due to limited scope for coral cover gains between the management and counterfactual scenarios as the number of outbreaking reefs declines. Similarly, as the average coral cover recovers to nearly 35% by 2026, reef state is close to the maximum carrying capacity of expected cover as predicted by ReefMod-GBR in the absence of COTS (~38% in 2026). A decline in coral cover thereafter due to climate-related impacts such as warming may also limit the scope for discriminating control-related gains in the long term.

CoCoNet results exhibited higher variability, and displayed the distinct signal of the new outbreak beginning in 2025. Benefits in terms of reduced proportions of outbreaking reefs were clear, especially as the old outbreak ended and the number of reefs outbreaking across the GBR dropped to a point where the control program had enough capacity to control all outbreaking reefs. The benefits in terms of coral cover were less clear, due to the underlying stochasticity of the model. This was driven by the fact that, in many cases, the variance due to stochastic forcing in CoCoNet was larger than the signal being generated by management scenarios over the short time scales considered. As a result, CoCoNet coral cover results should be interpreted cautiously. As outlined in the Discussion, CoCoNet was originally designed to reproduce medium to long-term system level dynamics, and over these timescales the signal due to control becomes clear as variability due to stochastic forcing asymptotes. However, because this study investigated scenarios capable of being reproduced by both ReefMod-GBR and CoCoNet, only shorter time horizons are reported.

## 3.1 Total amount of effort

### *3.1.1 CoCoNet*

When control effort was distributed across the entire GBR, CoCoNet results indicate that increasing the number of vessels from two, to five, and then eight provided benefits in terms of both reduced outbreaks at GBRMPA Priority Reefs (Figure 7a) and reefs across the GBR (Figure 7b) and, to a lesser degree, higher coral cover (Figure 7c). The results illustrate both the variability of the underlying biophysical model in CoCoNet, and the threshold effect of management effort compared to the number of Reefs being controlled.

Two vessels provided a substantial reduction in outbreaks on Priority Reefs (>20%; Figure 7a, left figure), but could only suppress outbreaks more broadly across the GBR during the early stages of the next outbreak when few reefs were outbreaking (Figure 7a, middle figure). There were also small gains in coral cover over this period, which rapidly diminished as the next outbreak developed. These patterns were amplified with additional vessels (Figure 7b and c), with 8 vessels providing near total suppression of outbreaks on priority reefs (Figure 7c, left figure) and maintaining a small significant improvement in coral throughout the outbreak.

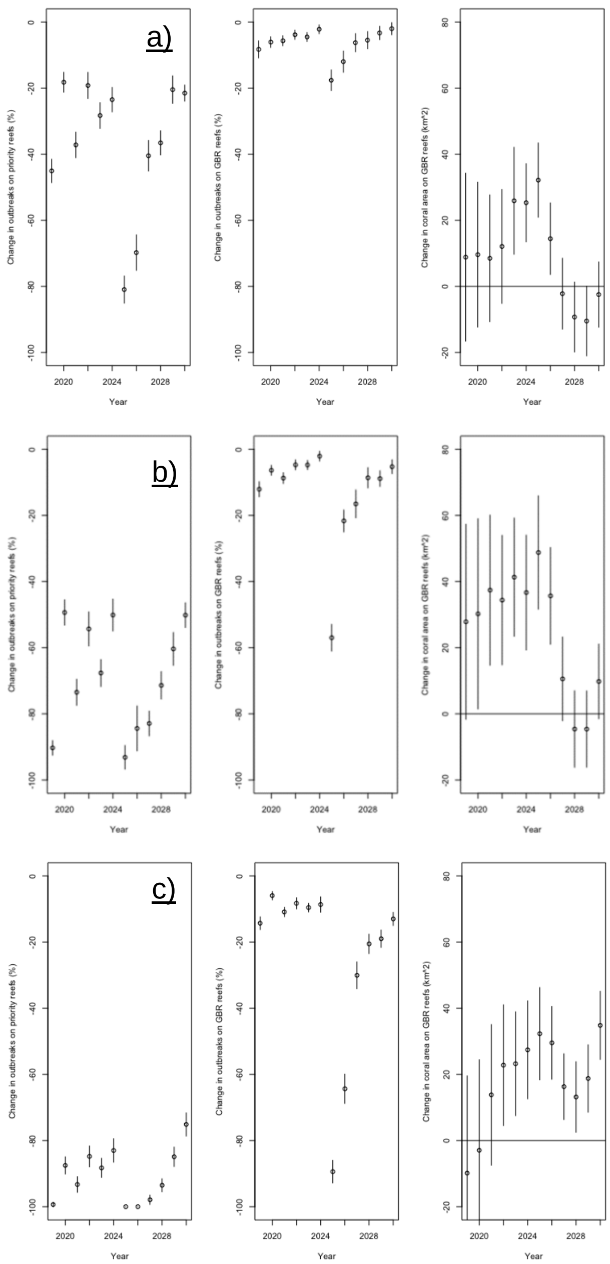


**Figure 7: Time-series of differences in CoCoNet between control scenarios and the no-control scenario for proportion of priority reefs with COTS outbreaks (left); proportion of all reefs with COTS outbreaks (centre); and increase in coral area (right). Scenarios corresponded to (a) 2 control vessels; (b) 5 control vessels; and (c) 8 control vessels. Each result is represented as a data point at the mean of the 50 ensemble runs, with error bars indicating the standard error across the ensemble.**

Importantly, the finding that: 1) a fleet of eight vessels could prevent outbreaks at over 80% of Priority Reefs; and 2) the proportion of Priority Reefs and other Reefs on the GBR where outbreaks were avoided increased roughly proportionally as the fleet size; suggested that marginal returns do not decrease at least up to an investment of eight vessels. Because eight vessels effectively avoided outbreaks on all Priority Reefs, further increases in fleet size would be unlikely to provide significant benefits on Priority Reefs, but would provide additional benefit more broadly across the GBR.

This same threshold effect is highlighted in the performance of the two vessel simulations; two vessels had a positive effect on coral cover and avoided outbreaks, but that was most clear when the current outbreak petered out and the next outbreak was only beginning around 2025. At that point in time, very few of the Reefs across the GBR were experiencing outbreaks, and the two vessels were sufficient to make a difference on that small number of Reefs. However, by 2028 they were overwhelmed as the number of outbreaking Reefs expanded beyond their capacity.

### *3.1.2 ReefMod*

Greater GBR-wide benefits were achieved with increased levels of effort (i.e. 2 < 5 < 8 boats). This trend was evident for both metrics of benefits: reduction in number of outbreaking reefs (Figure 8), and total coral cover area (Figure 9).

Both the five and eight Vessel strategy were able to protect practically all Priority Reefs from outbreaks; the eight Vessel strategy by 2024 and the five Vessel strategy by 2028 (Figure 8c). The eight Vessel strategy almost doubled the proportion of Reefs across the GBR at which outbreaks could be avoided by 2030, from around 20% of Reefs for the five Vessel strategy, to around 35% of Reefs for the eight Vessel strategy (Figure 8b). These results reflect those found with CoCoNet, although more clearly due to the lower underlying variability of ReefMod-GBR over the short timescales considered. These results suggest that the eight Vessel strategy is able to control both a greater number of total Reefs, and those Reefs it does control it controls earlier in the Program. In contrast, the two-vessel strategy both protected a small proportion of Reefs across the GBR from outbreak, and only gradually protected Priority Reefs over the duration of the simulation.

Strategies using five and eight Vessels delivered similar average benefits on total coral cover area across the GBR for the first two years, but from 2022 onwards the eight Vessel strategy was more effective. By 2026, deploying eight Vessels delivered up to 40% greater benefits compared to five Vessels (Figure 9B). Interestingly, not only was the eight Vessel strategy able to control more Reefs, tests showed that at the Reefs it did control it had a more positive effect on coral cover protected relative to the counterfactual scenario, presumably because Reefs were able to be protected sooner before they had already lost coral.

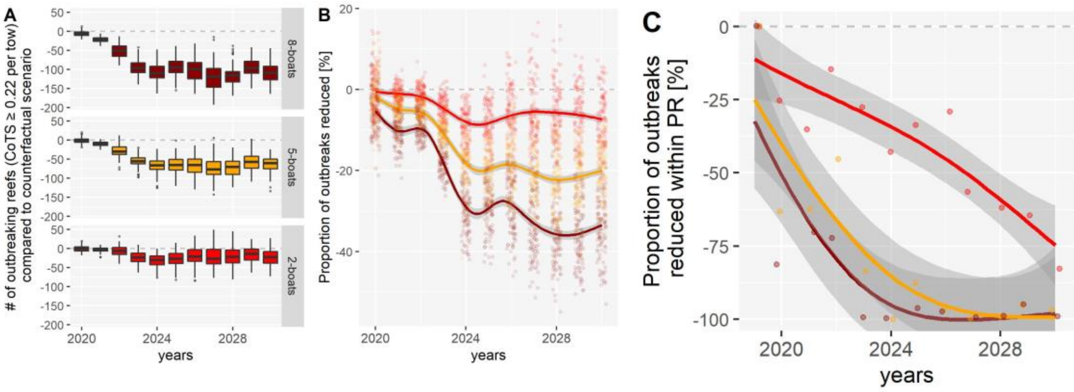


**Figure 8: Number of outbreaking reefs in ReefMod-GBR reduced with control (number of outbreaks in COTS control – counterfactual) over time (n=50 simulations for each scenario) for different levels of effort (boats=2 vs 5 vs 8). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits in terms of proportion of outbreaks relative to counterfactual. Data points represent each simulation. (C) Proportion of outbreaks reduced within Priority Reefs. Data points represent yearly averages. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

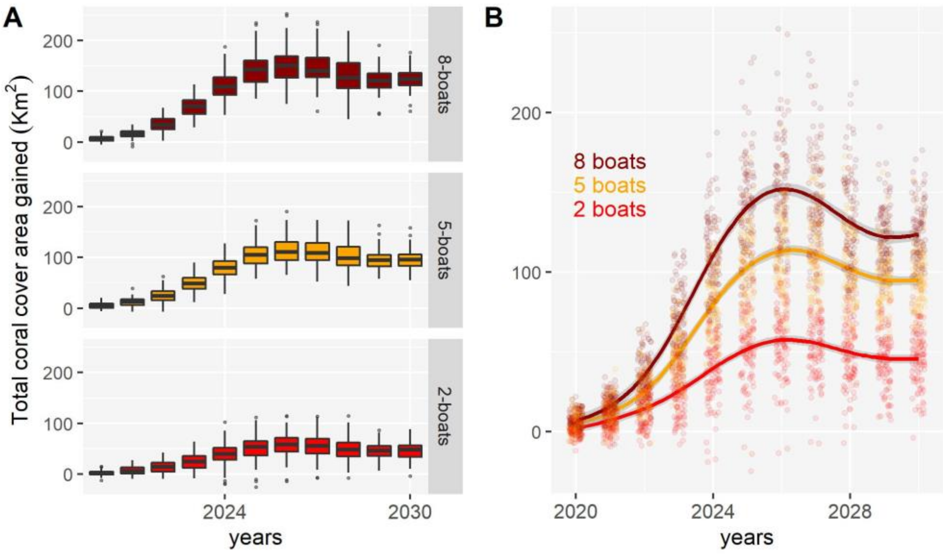


**Figure 9: Coral cover area km$^2$ benefits of control (COTS control – counterfactual) over time in ReefMod-GBR (n=50 simulations for each scenario) for different levels of effort (boats=2 vs 5 vs 8). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits output trends. Data points represent each simulation. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

## 3.2 Fixed spatial distribution of effort

### *3.2.1 CoCoNet*

There appears to be some benefit to focusing control efforts on particular regions of the GBR (cf. Figure 7b and Figure 10). While all regions provided comparable reductions in outbreaks on Priority Reefs and more broadly across the GBR, restricting control to the central region provided the most consistent increase in coral cover (Figure 10b, right figure). It should be noted that the significant overall variability of total coral cover from run-to-run within each ensemble (not shown in Figure 10) makes it difficult to draw strong conclusions related to absolute changes in coral cover from the CoCoNet results, although the differences between management scenarios seem significant relative to the standard error (indicated by the bars in Figure 10).

Given that all of the regions included the outbreak box, differences are thought to be mainly associated with the number of reefs being managed. Focusing on the central region allowed for effective protection of coral, whereas spreading the same effort over a much larger number of reefs left significant gaps in control. This contrast is most evident over the first couple of years of the control program (2019-2020) and again as the next outbreak becomes established (2029-2030). These were periods when outbreaks tended to be most numerous and focusing on a smaller number of reefs allowed control to be established more quickly.

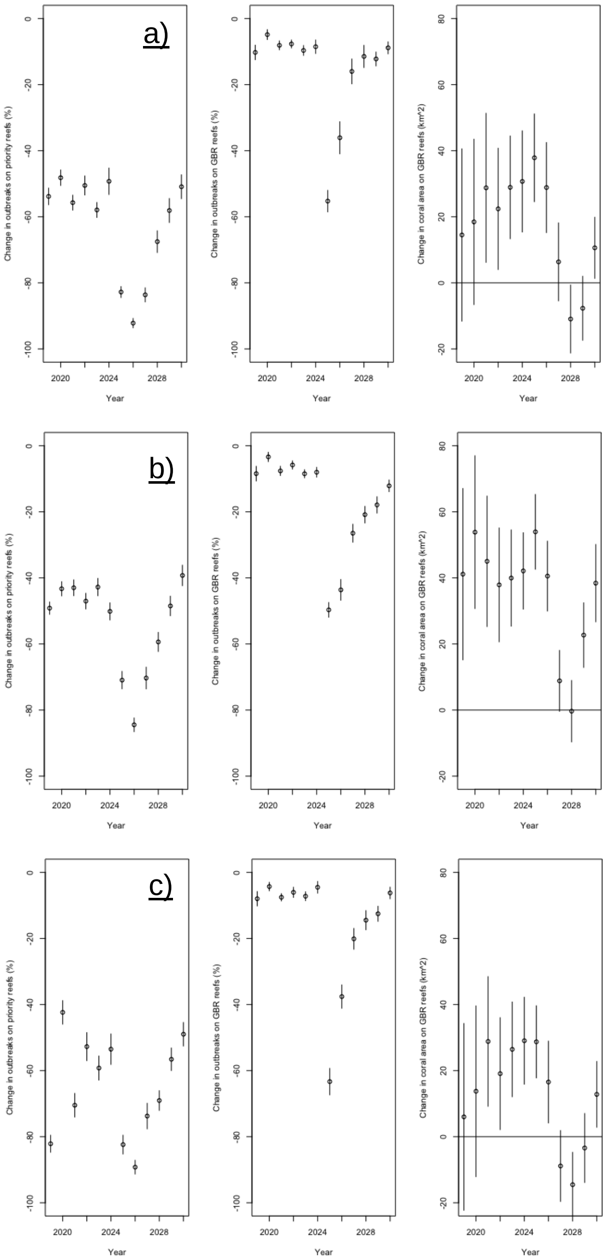


**Figure 10: Time-series of differences in CoCoNet between control scenarios and the no-control scenario for proportion of priority reefs with COTS outbreaks (left); proportion of all reefs with COTS outbreaks (centre); and increase in coral area (right). Scenarios corresponded to control focused within (a) the north and central regions; (b) the central region; and (c) the central and southern region.**

## *3.2.2 ReefMod*

Prioritizing a region appears to be more efficient in reducing the number of outbreaking reefs in the long term compared to a non-regional strategy (Figure 11). Specifically, focusing on Central reefs (14-21ºS) halved the number of outbreaking reefs across the GBR compared to a control strategy with no regional focus. During the last few years of simulations, the Central strategy controlled more reefs than any other regional strategy (up to 27% and 45% more reefs in 2027 and 2030, respectively; Figure 11b). Compared to the counterfactual scenario of no control, focusing on controlling Central reefs reduced, on average, 30% of the outbreaking reefs in 2030. Testing showed that the Central strategy provided greater total coral cover benefits when evaluating benefits among controlled reefs. As the number of controlled reefs for the Central strategy increased over time and more outbreaking reefs were treated at the end of the decade, the cumulative benefits of control increased for the Central strategy. In 2030, 93% of the visited reefs in the Central strategy were also visited that year in the eight Vessel strategy, which may explain why maximum coral cover benefits are comparable despite different levels of effort.

Model outputs suggest that management decisions based on spatial distribution of effort are less relevant when GBR-wide benefits are evaluated in terms of gains in total cover area (Figure 12), compared to when the objective is to reduce the number of outbreaking reefs (Figure 11). By 2030, no significant difference in total coral cover protected was evident among regional strategies (Figure 12) which show approximately 10% higher benefits than a strategy with no focal region.

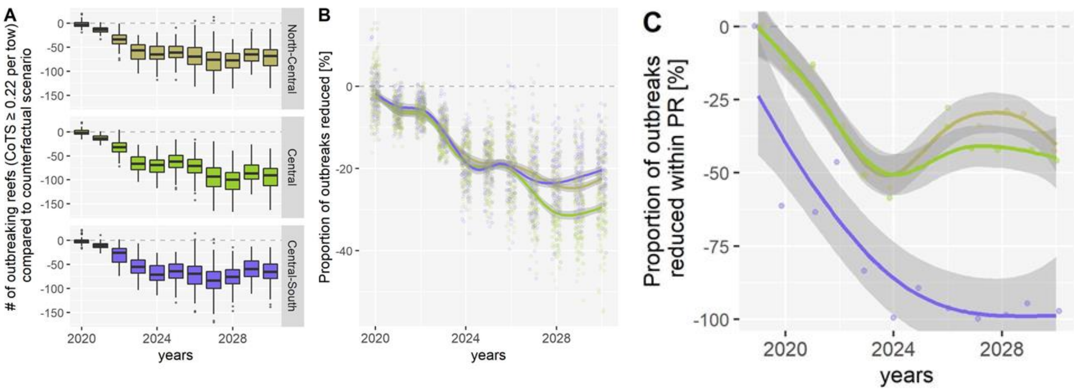


**Figure 11: Number of outbreaking reefs in ReefMod-GBR reduced with control (number of outbreaks in COTS control – counterfactual) over time (n=50 simulations for each scenario) for different focal regions (North-Central, Central, Central-South). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits in terms of proportion of outbreaks relative to counterfactual. Data points represent each simulation. (C) Proportion of outbreaks reduced within Priority Reefs. Data points represent yearly averages. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

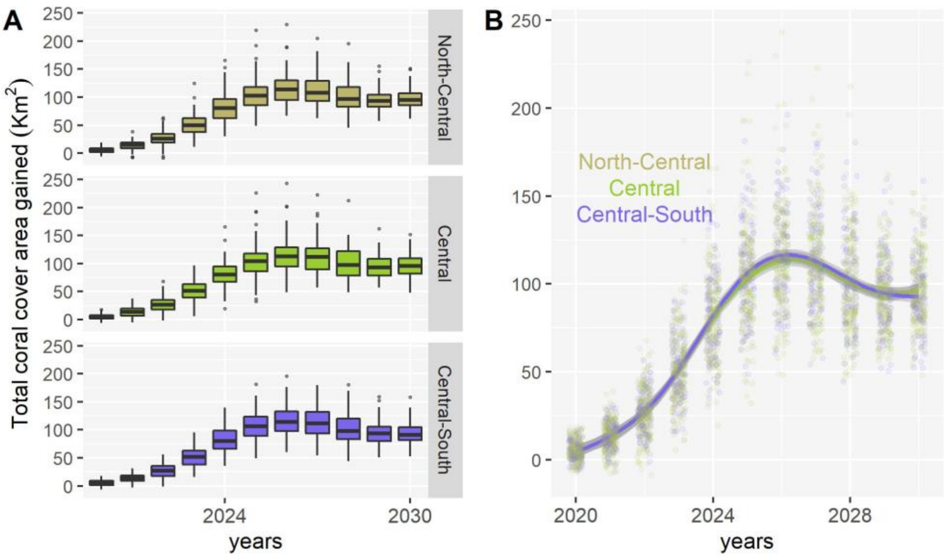


**Figure 12: Coral cover area km$^2$ benefits of control (COTS control – counterfactual) over time in ReefMod-GBR (n=50 simulations for each scenario) for different focal regions (North-Central, Central, Central-South). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits output trends. Data points represent each simulation. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

## 3.3 Responsive spatial-temporal distribution of effort

### *3.3.1 CoCoNet*

Prioritizing on areas near the outbreak front (i.e. within ± 1 degree of latitude) performed similarly to strategies that spread the same number of vessels across the GBR. Following the outbreak was slightly less effective in reducing outbreaks (cf. Figure 13 and Figure 7b), but generally preserved comparable to slightly increased coral cover (cf. Figure 13 and Figure 7c), within the range of standard error of the simulations.

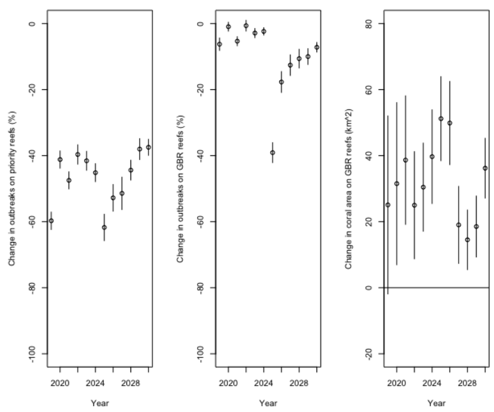


**Figure 13: Time-series of differences in CoCoNet between a control scenario and the no-control scenario for proportion of priority reefs with COTS outbreaks (left); proportion of all reefs with COTS outbreaks (centre); and increase in coral area (right). This scenario corresponded to control focused on a 2-degree wide latitudinal band centred on outbreaking across the northern and central regions (4 vessels) and another across the southern region (1 vessel).**

### *3.3.2 ReefMod*

Following the centre of the outbreak front was less effective than non-regional strategies and similarly effective to other regional strategies at reducing outbreaks within GBRMPA's Priority Reefs (Figure 14c). Across the GBR, it was approximately as effective as any other regional strategy at reducing outbreaks (Figure 14b). When GBR-wide benefits were measured in terms of total cover area gained it performed similarly to other regional strategies, and only marginally better than a non-regional strategy (Figure 15B).

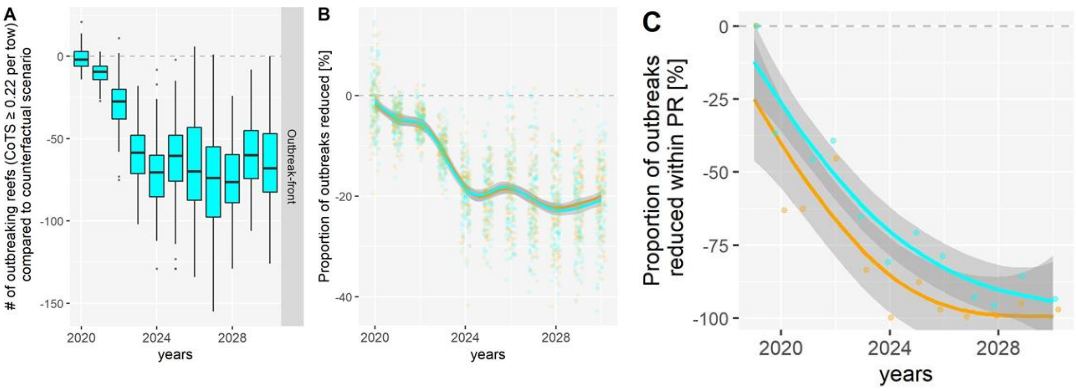


**Figure 14: Number of outbreaking reefs in ReefMod-GBR reduced with control (number of outbreaks in COTS control – counterfactual) over time (n=50 simulations for each scenario) for different focal regions (North-Central, Central, Central-South). (A) Box-and-whiskers plots showing the yearly variability across simulations for the 'Outbreak-front' control scenario (B) Comparison of benefits in terms of proportion of outbreaks relative to counterfactual Data points represent each simulation. (C) Proportion of outbreaks reduced within Priority Reefs. Data points represent yearly averages. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

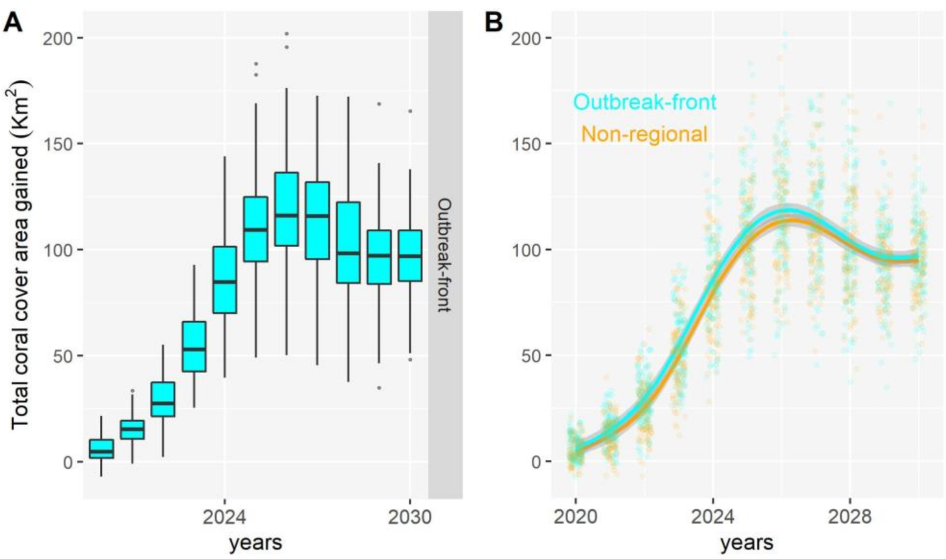


**Figure 15: Coral cover area km$^2$ benefits of control (COTS control – counterfactual) over time in ReefMod-GBR (n=50 simulations for each scenario) for the responsive distribution of effort (Outbreak-front). (A) Box-and-whiskers plots showing the yearly variability across simulations for the 'Outbreak-front' control scenario (B) Comparison of benefits output trends against a scenario of control with no-regional focus (orange, shown as 5-boats strategy in Figure 7). Data points represent each simulation. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

## 3.4 Triggers to pause and restart control

### *3.4.1 CoCoNet*

Restricting the control program to years when more than 10% of GBRMPA Priority Reefs were above the Ecological Threshold usually only suspended the program for a couple of years following the natural decline of an outbreak. During these years the cessation of control allowed some additional outbreaks to develop, although differences in coral cover tended to be minor, within the standard error of model runs (cf. Figure 16 and Figure 7b).

In the CoCoNet simulations, restricting control to outbreaking reefs (> 0.22 COTS per manta tow) was generally more effective in reducing outbreaks than basing control entirely on Site densities exceeding the Ecological Threshold (cf. Figure 16b and Figure 7b). These benefits were also reflected in significant gains in coral cover, which persisted throughout the control program. It appears that the restricting control to outbreaking reefs was effective in directing effort to where coral was being most rapidly predated, thereby maximising protection. Although the results appears to represent a distinct difference to the other management scenarios considered, generating benefits greater than the standard errors of the means of model runs, the potential impact of this result on overall levels of coral cover should be interpreted carefully, due to the high underlying variability in absolute estimates of total coral cover between model runs in CoCoNet.

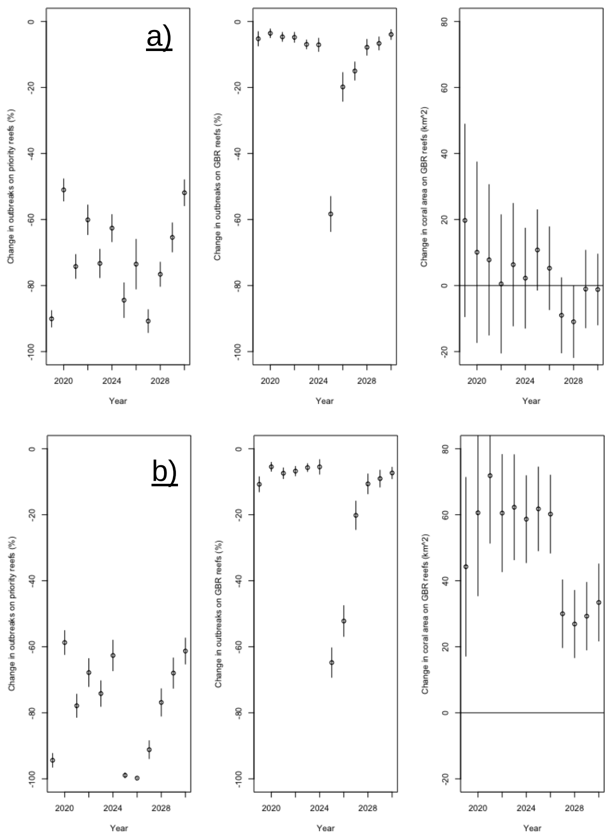


**Figure 16: Time-series of differences in CoCoNet between control scenarios and the no-control scenario for proportion of priority reefs with COTS outbreaks (left); proportion of all reefs with COTS outbreaks (centre); and increase in coral area (right). Scenarios corresponded to (a) control limited to years when more than 10% of priority reefs were outbreaking (> 0.22 COTS per manta tow); and (b) control limited to outbreaking reefs (> 0.22 COTS per manta tow).**

### 3.4.2 ReefMod

In contrast to the CoCoNet results, the greatest GBR-wide benefits were generated by the default scenario, with control triggered by Site-level COTS densities above the Ecological Threshold, rather than by Reef-level COTS densities (i.e. COTS ≥0.22 per tow) or a whole-of-GBR threshold (>10% of Priority Reefs above the Ecological Threshold). Compared to a scenario of control triggered at the Site-level, the effectiveness of control in minimizing COTS outbreaks was reduced by both the Reef-level and Global trigger, avoiding COTS outbreaks on 13% and 63% fewer reefs, respectively, by 2030 (Figure 17). In terms of total coral cover area benefits (Figure 18), relying on Reef-level COTS densities or a global threshold provided 26% and 40% less benefits compared to the default scenario triggered Site densities (Figure 18b).

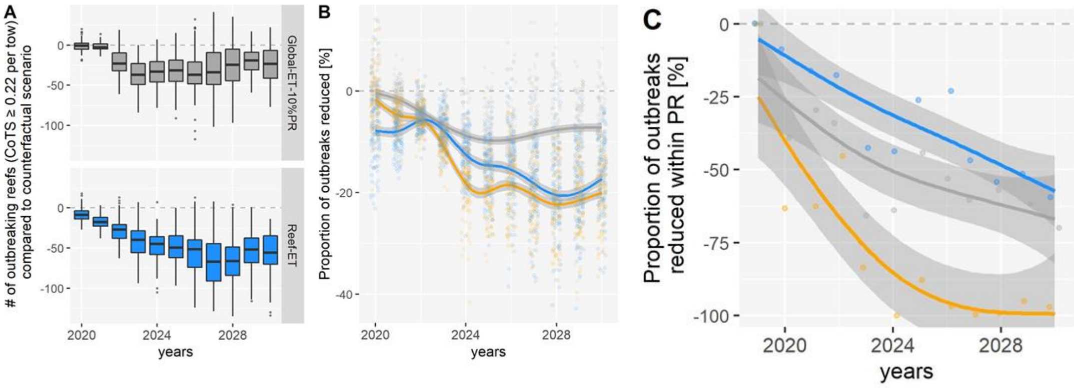


**Figure 17: Number of outbreaking reefs in ReefMod-GBR reduced with control (COTS control – counterfactual) over time (n=50 simulations for each scenario) using different triggers to initiate control (Global vs Reef-level). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits in terms of proportion of outbreaks relative to counterfactual. Data points represent each simulation. (C) Proportion of outbreaks reduced within Priority Reefs. Data points represent yearly averages. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

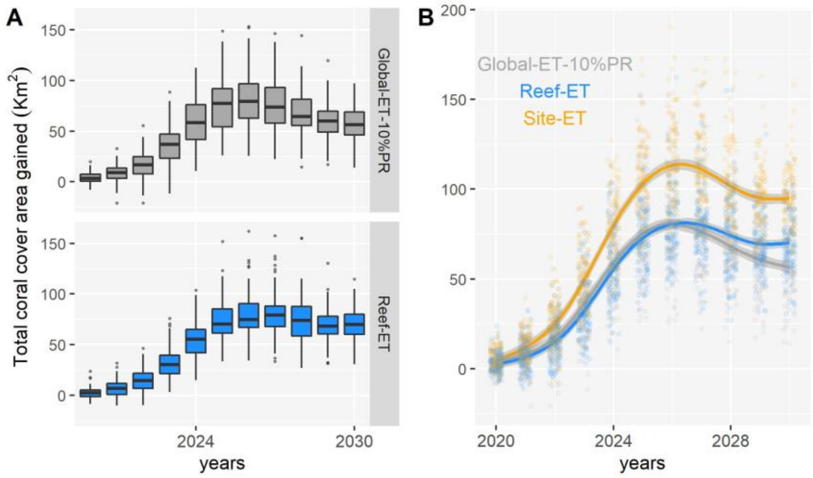


**Figure 18: Coral cover area km$^2$ benefits of control (COTS control – counterfactual) over time in ReefMod-GBR (n=50 simulations for each scenario) using different triggers to initiate control (Global vs Reef-level). (A) Box-and-whiskers plots showing the yearly variability across simulations for each control scenario (B) Comparison of benefits output trends against a scenario of control triggered at the site level (orange, shown as 5-boats strategy in Figure 7). Data points represent each simulation. Smooth lines represent the mean temporal trend (+/- 95% CI) per control scenario.**

# 4.0 DISCUSSION

The most important output of the body of work presented in this report is the development of a new regional-scale ensemble modelling capability for COTS management across the scale of the GBR. The capabilities of two complementary coral-COTS reef community models have been harmonised and extended with detailed descriptions of COTS control actions matching those used in the new Expanded COTS Control Program, providing ensemble predictions of regional scale outcomes of different control program strategies. The two models were originally built on fundamentally different foundations, and despite refinement so both capture all the same key biological processes from fine to large scales, they still reflect this in their different and complementary strengths; ReefMod-GBR employs tight empirical integration to underpin the sorts of short-term predictions considered in this report, while CoCoNet was originally built to describe medium-long term systems dynamics that will help predict the optimal progression of control into the next outbreak. The fact that the two models provide broadly similar management recommendations provides confidence that they will be robust to these types of variability. The results demonstrate the successful development of this capability, which will form a vital resource in continuing efforts to refine and improve the current Control Program, and to prepare for the next outbreak.

The results of the scenarios assessed by the extended CoCoNet and ReefMod-GBR models highlight three new advances in our understanding of the potential to control COTS at the regional scale on the GBR: 1) ecologically-meaningful regional-scale reduction of the proportion of reefs across the GBR experiencing outbreaks is possible with a manual Control Program similar to the one currently deployed; 2) the manner in which Control Program effort is distributed regionally across the GBR affects the efficiency and effectiveness of the Control Program, but positive outcomes are achieved as long as the core outbreaking areas are covered and effort can naturally flow to where it is needed through the scalable local-scale ecologically-informed process; and 3) maintaining control actions over time at the scale of the GBR is likely to outperform strategies that pause the Control Program when COTS densities drop, then restart it again at the start of the next outbreak.

These are significant and important results. There has long been a perception that effective COTS Control could only be implemented across small areas of reef (Birkeland & Lucas, 1990; Fisk & Power, 1999; Moran et al., 1988), and that these approaches would not scale to cover entire reefs (R. A. Kenchington & Pearson, 1982). This was supported by the outcome of the largest and longest running COTS Control Program to date, in Japan, where despite removal of approximately 13 million COTS between 1970 and 1983, COTS eventually killed greater than 90% of coral across vast areas of fringing reef. In contrast to this experience, early results from the first six months of the new Expanded COTS Control Program suggest that effective reef-scale COTS control has been achieved through the application of ecologically-informed control principles (Fletcher et al., 2020). However, this modelling report, and a companion report detailing an analysis of the potential of the new Control Program (Westcott, Fletcher, Gladish, MacDonald, & Condie, 2021), demonstrate for the first time that true regional-scale reduction of outbreaking COTS populations may be possible with realistic levels of Control Program investment, with 50 – 100% of GBRMPA Priority Reefs and 10 – 45% of all Reefs across the GBR prevented from outbreaking.

Equally important is the observation that this result is significantly degraded, by more than 63% in the case of the ReefMod-GBR results, if the COTS control effort is paused when COTS densities across the GBR fall between the end of one outbreak and the beginning of the next. This is important because, historically, this is how COTS control has been implemented on the GBR. After the first outbreaking reefs are detected around Cairns following outbreaks in the initiation box, it has taken several years to secure government funding for control efforts, which in turn have taken time to establish, and then have only been able to focus on a small number of high-value sites before funding is lost as outbreaks pass southwards of important tourism sites. Looking at the results of this analysis, there is no surprise that this approach yields unsatisfactory results. The population dynamics of COTS outbreaks are cumulative, and the results of this analysis show that the benefits of management are also cumulative. Consistent effort is required to reduce COTS outbreaks at individual reefs, and as more reefs are controlled, the resources available can be redirected to control remaining reefs.

Finally, although the proportional reduction in outbreaking reefs across the GBR varied based on the way control effort was distributed across GBRMPA Operational Regions, the variation was small relative to the overall reduction of COTS outbreaks provided by a five vessel Expanded COTS Control Program. In both the CoCoNet and ReefMod-GBR model results, the differences in the proportion of reefs prevented from experiencing COTS outbreaks between regional scenarios were significantly less than those for different fleet sizes. Coral cover results differed between the two regional scale models, with ReefMod-GBR projecting better performance over the modelled period from strategies encompassing both the Central and Southern Operational Region, while CoCoNet projected the highest benefits from a strategy focussing effort on the Central region. To some degree, these results are not surprising, as the Operational Regions are large, and the ecologically-informed local scale control program strategy outlined in Fletcher et al. (2020) is designed to generate ecologically-meaningful outcomes while naturally scaling to the amount of resources available within each Operational Region. More importantly, the results suggest that strategies that attempt to redirect control effort to the areas of highest COTS activity around the outbreak front do not outperform the strategies being employed in the Expanded COTS Control Program.

## 4.1 Effective regional strategies

### *4.1.1 Total effort*

Unsurprisingly, increased total effort yielded increased overall benefits. Importantly, the benefit in terms of proportional reduction in Reefs experiencing outbreaks and coral cover protected increased approximately linearly with total effort invested over the time periods modelled – i.e. in the ReefMod-GBR results in Figure 8 and Figure 9, the benefit generated by five vessels was approximately 150% that generated by two, and the benefit generated by eight vessels approximately 140% that generated by five. This suggests that although the current level of resourcing and distribution of effort can generate true regional-scale benefits, further investment would be likely to generate proportionally greater benefits. If we were approaching the point at which all reefs were effectively controlled, in contrast, the proportional difference in performance between the 8 and 5 vessel scenarios would be lower than that between the 5 and 2 vessel scenarios.

The exception to this is the list of Priority Reefs, which were controlled until almost all, in the ReefMod-GBR results, and most, in the CoCoNet results, of them no longer experienced outbreaks for fleets of both five and eight vessels. This may suggest that five vessels would be sufficient to effectively avoid COTS outbreaks across the current GBRMPA Priority Reefs. However, given differences in the strength of the results from the two models this bears further investigation before being used to inform critical decisions.

Even though the two model platforms deliver differing specific results across the scenarios runs, they deliver the same ranking of results and broadly the same message. The variance between CoCoNet runs makes it difficult to identify clear effects on coral cover, but the effects on avoided outbreaks are clear, and tell a similar story to ReefMod-GBR: a fleet of two vessels could prevent outbreaks on only a small proportion of both Priority Reefs and Reefs across the GBR; five vessels could make a meaningful difference across the GBR and protect a significant proportion of the Priority Reefs from outbreaks; and a fleet of eight vessels could protect 50% more Reefs across the GBR from outbreaks than a fleet of five, and essentially all the Priority Reefs.

In interpreting these results for future outbreaks, it is important to note that the scenarios considered here modelled an outbreak that began in 2010 with control beginning in 2019. Therefore, these results represent an outcome far more conservative than: 1) what might have been achieved had the new Expanded COTS Control Program been in place from 2010; 2) what actually happened with control implemented between 2012 – 2018; and 3) what could be achieved during the next outbreak. In the modelled scenarios, the outbreak had a significant chance of spreading and causing damage before management was implemented. Moreover, it is likely that the benefits of the new Expanded COTS Control Program, had it begun at the start of the current outbreak, are significantly underestimated, due to the cumulative effect of both COTS impacts and the benefits of management. Put simply, effective control in 2010 would have reduced the size of the outbreak and amount of control required in 2011, which would have further reduced the outbreak and required control in 2012, and so on. Although not part of the current analysis, preliminary results investigating this scenario suggest that, had the new COTS Control Program been implemented from 2010, by 2019 the amount of control available with a fleet of five or eight vessels could be maintaining ecologically-meaningful outcomes distributed across many hundreds of reefs. This potential is considered, empirically, in the companion NESP report *Integrated Pest Management Crown-of-Thorns Starfish Control Program on the Great Barrier Reef: Current Performance and Future Potential* (Westcott et al., 2021).

### *4.1.2 Fixed spatial distribution of effort*

The outcomes of the models were not as sensitive to the regional spatial distribution of effort as to the total number of vessels in terms of the proportion of reefs at which outbreaks were avoided, nor in the total amount of coral cover protected across the GBR.

The ReefMod-GBR results showed that a strategy that focussed the efforts of five vessels on the Central region could reduce the proportion of Reefs outbreaking across the GBR to almost the level predicted for the eight-vessel fleet in scenario 8b-GBR by 2030. However, in terms of the Priority Reefs, only the Central-Southern scenario was able to avoid all outbreaks at Priority Reefs by 2030, presumably due to the southward spread of the outbreak as the simulations progressed. In neither case was the total area of coral cover protected significantly improved over the North-Central strategy, or the five-vessel whole-of-GBR scenario considered (5b-GBR).

The CoCoNet simulations tell a similar story in terms of avoided outbreaks: the proportional reduction in outbreaking reefs is maximised for the southern-central strategy in the lead up to the end of the current outbreak; but a slightly different story in terms of coral protected, which is maximised for a strategy focussed on the Central Operational Region. As with the ReefMod-GBR results, the first of these factors likely reflects the southward progression of the outbreak for the period over which results are presented, while the latter probably reflects the average size of the Reefs in the central region.

It is again important to consider the impact of the modelled scenarios starting management in 2019, by which point the outbreak was focused in the Central region. If scenarios modelling management beginning in 2010 had been considered, it is likely that the performance of the North-Central strategy may have been significantly improved due to the cumulative benefits of reducing early COTS outbreaks on northern Reefs and reducing subsequent larval dispersal to the Central region later in the outbreak. In contrast, when the scenarios modelled started management in 2019, few northern reefs were experiencing COTS outbreaks, so the North-Central strategy considered simply pulled Control Program resources away from the Reefs outbreaking in the Central region. Further investigation will be necessary before the conclusions of this analysis are applied to future outbreaks.

### *4.1.3 Responsive spatio-temporal distribution of effort*

While distributing effort across Operational Regions yielded some small positive differences in performance, a more complicated scenario in which the progression of the outbreak southwards along the GBR was calculated each year and control effort distributed in a band ±1° of latitude either side of the centre of the outbreak front did not provide any additional benefits. This is a useful result in that it suggests that the Operational Regions currently employed by GBRMPA in the Expanded COTS Control Program are an effective manner of distributing effort across the GBR, and that more advanced strategies are not required.

In both the CoCoNet and ReefMod simulations, the responsive strategy performed similarly, within standard error, to strategies using fixed distributions of effort across the GBR. In CoCoNet, following the outbreak was slightly less effective in reducing outbreaks, but preserved slightly more coral cover than the same number of vessels distributed across the GBR. In ReefMod, following the outbreak was less effective than non-regional strategies and similarly effective to other regional strategies at reducing outbreaks within GBRMPA's Priority Reefs and maintaining coral cover. It is possible that this result underestimates the benefit of a responsive strategy, because modelled scenarios only considered management beginning in 2019, by which point the outbreak front was south of latitude 17° S. It will be important to model the impact of management starting earlier in the outbreak progression before reaching firm conclusions about the benefits of dynamically adjusting spatial distribution of effort.

This is also an interesting result because it runs counter to outcomes reported elsewhere in the pest management literature, which often recommend boundary zones at or ahead of the outbreak front for slowing the spread or containing outbreaks (Cacho, Wise, Hester, & Sinden, 2008; Fletcher, Westcott, Murphy, Grice, & Clarkson, 2015; Alexei A. Sharov & Andrew M. Liebhold, 1998; A. A. Sharov & A. M. Liebhold, 1998; Sharov, Liebhold, & Roberts, 1998). The likely reasons for this are related to COTS outbreak ecology and the specific management scenarios considered. Ecologically, COTS outbreaks are spread across a wide region with the potential for many individual outbreaking meta-populations at a single point in time. In terms of management, the scenarios considered structured effort at two scales: 1) the broad scale of management regions or the outbreak front; and 2) the fine scale mediated by the ecologically-informed local-scale decision tree process outlined in Fletcher et al. (2020). On one hand, the broad scale of the COTS outbreak front meant that the spatio-temporal strategy needed to cover a large area and therefore could not provide significant performance improvements by focussing the area over which management was applied at the broad scale. On the other, the decision tree process was able to target fine scale actions effectively whether at the scale of an Operational Region or of the outbreak front. The net effect of these two processes was that dynamically targeting management effort around the outbreak front did not outperform strategies applying fixed spatial distributions of effort.

Importantly, these results show that the ecologically-informed local-scale control strategies outlined in Fletcher et al. (2020) are effective at distributing effort within Operational Regions to generate ecologically-meaningful outcomes at the regional scale. That decision tree process is designed to rapidly and efficiently move past Reefs with low densities of COTS, and invest proportionally more effort at Reefs with high densities of COTS, which will generally be found near the outbreak front. Despite the fact that the Central region spans seven degrees of latitude, no significant improvement over the combination of Operational Region focus, Priority Reef identification, and local-scale decision support was realised by further focussing Control Program actions to the two degrees directly around the outbreak front.

### *4.1.4 Triggers to start and stop control*

The other vital result of this analysis is that pausing the Control Program at the end of an outbreak when average COTS density across the GBR dropped below the relevant Ecological Threshold was a mistake. In the ReefMod-GBR results, 63% fewer reefs were prevented from experiencing outbreaks, and 40% less coral cover was protected. In the CoCoNet results the effect was less pronounced, but control was typically only paused for a couple of years, and led to a reduction in the proportion of reefs at which outbreaks were avoided.

The nature of the effect is much less clear when a trigger for control is applied at the scale of the average COTS density over a Reef. In the ReefMod-GBR results, the reduction in outbreaking Reefs was reduced by 13% over the default strategy aiming to reduce every Site to the Ecological Threshold, and a smaller proportion of Priority Reefs, in particular, were prevented from outbreaking. This is likely to be related to the fact that the Reef-level threshold of an average of 0.22 COTS/tow is the same as the definition used to determine whether a Reef is outbreaking; in this scenario Reefs are reduced to barely below outbreak status and then control immediately moves on, allowing COTS populations to recover and putting the Reef back into the outbreak category.

However, in CoCoNet, using a Reef trigger provided a small overall improvement in the proportion of Reefs at which outbreaks were avoided, and a significant improvement in coral cover maintained across the GBR. This result is probably driven by the fact that the Reef-scale trigger to end control allows the less efficient tail-end of control activities to wrap up at each Reef sooner, leaving a small number of Sites above the Ecological Threshold, but allowing the Control Program to move onto the next Reef where it can protect more coral.

These outcomes represent a fundamental tension in any pest management program; control the most easily located pests across large areas, leaving many still in the landscape to reproduce and rebuild the pest population, or do a more thorough job over a smaller area. The fact that the two model frameworks produce contrasting results probably relates to the details with which they are implemented. ReefMod-GBR used a six month time step but averaged results once a year in a way that may have allowed populations at Reefs reduced just to the Ecological Threshold at the six-month time step to recover enough to push them back into outbreak status by the time results were aggregated at the twelve-month time step. CoCoNet, in contrast, avoided this complexity because the annual management and COTS population time step were synced, and the additional area covered by the Reef-Threshold strategy outweighed any potential negative effects. In the end, the optimal answer to this question for regional scale management of COTS will depend on the detail included in each model, and will require further investigation.

However, the key message: that pausing the Control Program when COTS densities fall across the GBR is a poor strategy, is clear. It is unlikely to be significantly modified by the fact that all the scenarios modelled considered management beginning in 2019. It is therefore an important observation as preparations continue for the next COTS outbreak, which is expected to begin in the mid-2020s.

## 4.2 A regional-scale modelling capability

The analysis shows that the current Expanded COTS Control Program is on track to produce the outcomes for which it was designed: prevention of COTS outbreaks and protection of coral cover at high Priority Reefs within the GBR. It also shows that the Expanded COTS Control Program's current design, based around the automatically-scaling local-scale ecologically-informed Control Program outlined in Fletcher et al. (2020), with control efforted distributed across Operational Regions and targeted at GBRMPA Priority Reefs, is an effective strategy to achieve regional outcomes and does not need to be modified with more complicated dynamic regional strategies. However, the results also point to several places where the two model frameworks diverge, and several strategically important opportunities where the capability that has been developed as part of the NESP COTS Regional Scale Modelling work can be leveraged to deliver significant benefits to the future Control Program.

The current analyses demonstrate that both models can broadly reproduce the details of COTS on the GBR, the description of various management strategies at the regional scale, and the cumulative interactions of management and COTS population dynamics over years and decades. Both models describe the key biological relationships between COTS and coral communities across the scale of the GBR, and despite the models implementing COTS population processes in fundamentally different ways, both reproduce the broad scale dynamics and periodicity of GBR-scale outbreaks. At the same time, the two model frameworks vary in the level of detail with which they describe different parts of the system (Table 2) and, as a result, produce quantitatively different results at short- and long-time scales.

**Table 2: Comparison of the characteristics of ReefMod-GBR and CoCoNet.**

| **Model features/processes** | **ReefMod-GBR** | **CocoNet** |
|---|---|---|
| Time step | Seasonal (6 months) | Annual (12 months) |
| Model domain | GBR (3806 reefs) | GBR (3753 reefs) |
| Resolved spatial structure | One patch of 20 x 20 cells (each 1 $m^2$), extrapolated to each reef | Every dive site (~14 ha) on every reef |
| Number of coral groups | 6 | 5 |
| Coral representation | Individuals from each group | Cover of each group |
| Size-dependent coral fecundity, growth and mortality (individual corals) | Yes | No |
| Density-dependent coral recruitment | Yes | Yes |
| Coral-coral competition | Yes | Yes |
| Coral-algal competition | Yes | No |
| Effects of sediments on coral | Larval and juvenile mortality plus reduced growth | Reduced growth |
| Effects of rubble on coral | Juvenile mortality | Space limitations |
| Effects of ocean acidification on coral | None | Reduced growth |
| Hydrodynamics for coral larval dispersal | eReefs GBR-4 km | eReefs GBR-1 km |
| COTS size/age classes | 6-month age classes up to 8+ years old) | 12-month age classes up to 5+ years old) |
| Density-dependent COTS recruitment | Yes | Yes |
| Size-dependent COTS fecundity and coral consumption | Yes | Yes |
| COTS population collapse | Cover of coral preferred by COTS < 5%, or outbreak duration > 2-5 years (set randomly for each reef) | Outside of ‘outbreak box’ COTS concentrations halved one year prior to recorded start of all historical outbreaks and then every 17-years |
| Hydrodynamics for CoTS larval dispersal | eReefs GBR-4 km | eReefs GBR-1 km |
| Calibration of cyclone impacts | Empirical | Empirical |
| Cyclone dynamics pre-2020 (hindcast) | Reef exposure to past cyclones (2008-2020) | Reef exposure to past cyclones (1985-2020) |

| | | |
|---|---|---|
| Cyclone dynamics post-2020 (forecast) | Random selection of synthetic cyclone tracks | Statistical probability of cyclone categories |
| Calibration of coral bleaching impacts | Empirical | Empirical |
| Bleaching exposure pre-2020 (hindcast) | Reef exposure to past DHW (2008-2020) | Reef exposure to past DHW (1985-2020) |
| Bleaching exposure post-2020 (forecast) | Downscaled projections (2020-2070) of climate model MIROC (RCP 2.6) | Statistical projection of future ocean heat-waves (RCP 2.6) |
| Forcing with coral survey data | Individual reefs initialised (2008) with AIMS-LTMP coral cover and community composition (214 reefs) | No – results post 1980 were insensitive to initial conditions |
| Forcing with COTS survey data | Individual reefs initialised with adult COTS density predictions from CoCoNet (2008); observed adult COTS density (AIMS, RHIS, FMP) overriding model predictions at individual reefs/years (2008-2018) | No – results post 1980 were insensitive to initial conditions |
| Independent model validation | Predictions of total coral cover (2009-2018) confronted with 67 AIMS-LTMP sites | Predictions of total coral, COTS densities and COTS outbreak rates (2009-2019) confronted with all available AIMS-LTMP data. |

Both models follow the dynamics of COTS populations over periods of years across almost all reefs on the GBR, but vary in the time step they use (ReefMod-GBR: 6 months; CoCoNet: 12 months), and the total number of reefs they cover (ReefMod-GBR: 3806; CoCoNet: 3753). ReefMod-GBR uses a description of individual coral colonies scaled to estimate coral population dynamics at a Reef, while CoCoNet follows overall coral population dynamics at Sites within a Reef. Both incorporate historical and projected cyclone and bleaching events, but use different extents of historical data and slightly different future projections in doing so.

These differences are not unique to the way the two model systems describe COTS or COTS management; they have been identified in their use elsewhere on the GBR. For instance, ReefMod-GBR typically provides higher average coral cover estimates across the GBR than CoCoNet for similar initial conditions, even when COTS control is not incorporated in either model (Condie, pers. comm.), so it is unsurprising that it predicted larger coral cover gains from the strategies considered here. Importantly, however, although the two model frameworks differ in the magnitude of the results they project, the relative performance of the various regional-scale strategies was generally well aligned.

This highlights one benefit of developing two complementary regional scale modelling capabilities: disparate modelling techniques that deliver the same management recommendations provide confidence that the recommendations are valid despite the variability typically exhibited by simulation models incorporating significant external drivers, like bleaching events and cyclones. This ensemble approach is a well-developed technique in climate modelling, but less often applied to ecological modelling (Gårdmark et al., 2013). Having two regional-scale coral-COTS reef community models incorporating realistic management strategies is an important resource, and will be vital to improving the control of COTS at regional scales on the GBR in future. The complementary models developed as part of this work clearly demonstrate that regional-scale COTS control can reduce the proportion of reefs that experience outbreaks, and that control must be ongoing, because both the costs of COTS outbreaks and the benefits of management distributed across the GBR accumulate and are magnified over time. However, the scale of the benefits they project in terms of coral protected are quite different.

Most obviously, CoCoNet produced lower estimates of coral cover gains due to control activities than ReefMod-GBR, as expected based on their underlying coral-COTS reef community models. For instance, CoCoNet predicted around 20 $km^2$ coral would be protected with a GBR-wide control strategy with eight vessels, compared to ReefMod-GBR's estimate of ~150 $km^2$. However, without COTS control, ReefMod-GBR predicts close to 30% coral cover, whereas CoCoNet predicts closer to 22%. For the approximately 20,000 $km^2$ of coral on the GBR, this equates to a difference of 1,600 $km^2$ between the two models before COTS control is taken into account. Each model compares each scenario to its own counterfactual, which should correct for much of this difference, but due to the large overall differences in coral cover estimates, even small differences in the way that coral cover is accounted for between the models could be expected to yield significantly smaller benefits from CoCoNet than ReefMod. Reliably resolving these small differences from such large background variation may require many more Monte Carlo iterations than the model frameworks have currently employed.

The number of model iterations required is likely to vary across the two models, due to the fact they exhibit different levels of variance between model runs. CoCoNet exhibited significantly higher variability in its results than ReefMod-GBR. The variance across coral cover benefits across 50 CoCoNet runs was typically 80 – 200 $km^2$; for ReefMod-GBR it was typically 50 – 80 $km^2$. This is unsurprising given the way CoCoNet implements stochastic events, such as bleaching and cyclones, and its focus on reproducing realistic system dynamics over the course of an entire outbreak. Over the short time scales considered in this report, this often made it difficult to identify statistically significant distinctions between coral cover estimates in the CoCoNet results. ReefMod-GBR, in contrast, used an empirical fit to real world data, where available, up to the start of the modelled period, before implementing a stochastic disturbance regime following climate projections. This produced lower variability in the results over the short time period considered, which made it easier to interpret results, but would, perhaps, underestimate the variability in strategy performance over long times frames, such as may be considered for a new outbreak.

In contrast, the CoCoNet results captured the impact of the end of the current outbreak a lot more clearly than ReefMod-GBR. The exact processes by which outbreaks end on both individual Reefs and the GBR represent a key gap in ecological knowledge of COTS outbreaks, and the two models implemented the process differently: CoCoNet exhibits a natural decline in COTS populations as coral resources decline, and adds a fixed mortality rate across age-size classes at the end of an outbreak; while ReefMod-GBR implements a size-dependent rate representative of lack of food or disease processes prevalent at the end of an outbreak. As the analysis covered the period where the current outbreak is expected to end, it is inevitable that these differences were apparent in the results presented.

To some degree, these differences reflect the strengths of each model; CoCoNet was developed out of attempts to describe large-scale long-term system dynamics, while ReefMod-GBR grew out of a detailed modelling of coral communities within reefs to achieve a realistic reproduction of large-scale coral dynamics. As such, it is unsurprising that the two models produce different results but, as noted above, the fact that the broad outlines of those results remain the same is a powerful outcome in itself. It also presents an opportunity to refine each of the models using the lessons learned in the other.

Now that this capability has been developed, the most immediate need is to consider optimal regional scale responses to the next outbreak expected to begin in the initiation box in the mid-2020s. The functionality developed as part of the NESP Regional Scale Modelling work can be efficiently extended to consider the likely effects of regional strategies when control is implemented from the very beginning of an outbreak. It is possible that, due to the cumulative effects of management actions, targeted regional control efforts at the current level of resourcing applied at the very beginning of an outbreak could reduce the impact of COTS at the scale of the entire GBR. Given this potential, it is vital that regional modelling capability is extended as necessary and applied to this question.

Once this capability is extended, the regional strategies considered in the current analysis should be assessed for a Control Program beginning at the start of an outbreak. Although the current analysis shows that more complicated spatial distributions of effort are unlikely to significantly improve outcomes for the current outbreak, that may not be the case when control starts earlier in the outbreak. Developing the regional scale modelling capability required significant investment during the NESP research project; now that is available, it should be leveraged to test a wider range of regional strategies, because small increases in efficiency can generate large benefits or savings once scaled to the entire Control Program.

Finally, this regional scale modelling capability should be leveraged to provide recommendations on GBRMPA's regional reef prioritisation process. While the current GBRMPA process is a dramatic improvement on historical approaches to target COTS control on the GBR, it still essentially provides a "snapshot" process each year, with a component related to the potential for larval spread from individual reefs. In contrast, the regional scale modelling capability developed as part of this work can provide a truly dynamic picture of the benefit of control at each reef, and how that benefit accumulates at downstream reefs in subsequent years.

# 5.0 SUMMARY AND RECOMMENDATIONS FOR MANAGERS

The most important outcome of this research is the development of a new regional-scale ensemble modelling capability for COTS management across the scale of the GBR. Two complementary coral-COTS reef community models originally developed for distinct purposes have been harmonised and extended with detailed descriptions of control actions matching those currently employed in the Expanded COTS Control Program, providing ensemble predictions of regional scale outcomes of different control program strategies. This will be a vital resource in continuing efforts to refine and improve the current Control Program, and to prepare for the next outbreak.

The results also suggest that the current regional strategies being employed in the Expanded COTS Control Program are likely to generate ecologically-meaningful regional scale reductions in the proportion of reefs experiencing COTS outbreaks across the GBR, including most of GBRMPA's identified Priority Reefs. None of the alternative strategies for regional distribution of effort considered are likely to provide significant increases in performance during the current outbreak, other than increasing the number of vessels in the fleet. However, strategies that pause the Control Program as average COTS densities fall at the end of an Outbreak perform significantly worse as the next Outbreak picks up.

Even more optimistically, the regional management scenarios modelled as part of this study, with control actions beginning at the start of the new Expanded COTS Control Program in 2019, make assumptions conservative compared to what has actually been implemented on-water since 2012, and what could be achieved if control were to begin at the onset of a COTS outbreak. Given the cumulative benefits of management actions early in an outbreak, this suggests that the strategies currently being employed in the Expanded COTS Control Program could, if they are maintained, make significant impact on the next outbreak, expected to begin in the mid-2020s.

## 5.1 Recommendations for managers

### *5.1.1 In the immediate future: continue with the current strategy*

The current ecologically-informed Expanded COTS Control Program is working, both at the scale of individual reefs, as shown by previous analyses (Fletcher et al., 2020), and regionally, as shown by the analyses here and in the companion NESP TWQ Hub report on Control Program effectiveness and potential (Westcott et al., 2021). None of the alternative regional-scale strategies considered in this report meaningfully outperformed the strategies currently being employed, so the Expanded COTS Control Program should continue implementing the current strategy.

### *5.1.2 In the short-term: leverage our regional modelling capability*

The ensemble regional scale modelling capability developed as part of this project should be leveraged to provide:

1) an assessment of whether the regional-scale impacts of the next outbreak can be largely avoided through the current strategy, and what level of resources would be required to achieve that outcome;
2) if the regional scale impacts of the next outbreak cannot be completely avoided, recommendations on optimal regional strategies when control begins at the start of an outbreak; and
3) guidance on which Priority Reefs to target for control within each GBRMPA Operational Region in order to maximise the accumulative regional-scale benefits of control at specific reefs

### *5.1.3 In the medium-term: don't stop the Control Program between outbreaks*

The next outbreak is expected to begin on reefs in the initiation box north of Cairns in the mid-2020s. The results of this analysis show that strategies that attempt to reduce the costs of control by pausing control efforts when COTS densities start to drop at the end of the current Outbreak bring with them the risk of a significant reduction in Control Program effectiveness over the next decade compared to strategies that continue targeting high density aggregations of COTS even when average densities across the GBR are low. Both the costs of COTS impacts and the benefits of COTS control accumulate over time; pausing the Control Program today will affect how many reefs can be prevented from outbreaking tomorrow.

# REFERENCES

Babcock, R., & Mundy, C. (1993). *Seasonal changes in fertility and fecundity in Acanthaster planci* Paper presented at the The Possible cause and consequences of outbreaks of the crown-ofthorns starfish. , Proceedings of a workshop held in Townsville, Queensland, Australia.

Babcock, R., Plaganyi, E., Morello, E., Rochester, W., Hoey, J., Pratchett, M., & Anthony, K. (2014). *What are the important thresholds and relationships to inform the management of COTS? Draft report, 30 June 2014*. Retrieved from Australia: http://hdl.handle.net/11017/2955

Babcock, R. C., Milton, D. A., & Pratchett, M. S. (2016). Relationships between size and reproductive output in the crown-of-thorns starfish. *Marine Biology, 163*(11), 234. doi:10.1007/s00227-016-3009-5

Babcock, R. C., & Mundy, C. N. (1992). Reproductive biology, spawning and field fertilization rates of Acanthatser planci. *Mar. Freshwater Res., 43*(3), 525. doi:10.1071/mf9920525

Babcock, R. C., Mundy, C. N., & Whitehead, D. (1994). Sperm Diffusion Models and in situ Confirmation of Long-Distance Fertilization in the Free-Spawning Asteroid Acanthaster planci. *Biological Bulletin, 186*(1), 17. doi:10.2307/1542033

Babcock, R. C., Plagányi, É. E., Condie, S. A., Westcott, D. A., Fletcher, C. S., Bonin, M. C., & Cameron, D. (2020). Suppressing the next crown-of-thorns outbreak on the Great Barrier Reef. *Coral Reefs*. doi:10.1007/s00338-020-01978-8

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

Barnes, J. H. (1966). The crown-of-thorns starfish as a destroyer of coral. *Australian Natural History, 15*, 257-261.

Birkeland, C., & Lucas, J. S. (1990). *Acanthaster planci: major management problem of coral reefs*. Boca Raton, Florida: CRC press.

Bozec, Y.-M., Hock, K., Mason, R. A. B., Baird, M. E., Castro-Sanguino, C., Condie, S. A., . . . Mumby, P. J. (2020). Cumulative impacts across Australia's Great Barrier Reef: A mechanistic evaluation. *bioRxiv*, 2020.2012.2001.406413. doi:10.1101/2020.12.01.406413

Bozec, Y.-M., & Mumby, P. J. (2019). *Detailed description of ReefMod-GBR and simulation results*. Retrieved from Townsville, Australia: https://gbrrestoration.org/wp-content/uploads/2020/09/T6-Modelling-Methods-and-Findings_26April_FINAL3.pdf

Breiman, L. (2001). Random Forests. *Machine Learning, 45*(1), 5-32. doi:10.1023/A:1010933404324

Brodie, J., Fabricius, K., De'ath, G., & Okaji, K. (2005). Are increased nutrient inputs responsible for more outbreaks of crown-of-thorns starfish? An appraisal of the evidence. *Marine Pollution Bulletin, 51*(1–4), 266-278. doi:http://dx.doi.org/10.1016/j.marpolbul.2004.10.035

Bruno, J. F., & Selig, E. R. (2007). Regional Decline of Coral Cover in the Indo-Pacific: Timing, Extent, and Subregional Comparisons. *PLoS ONE, 2*(8), e711. doi:10.1371/journal.pone.0000711

Cacho, O. J., Wise, R. M., Hester, S. M., & Sinden, J. A. (2008). Bioeconomic modeling for control of weeds in natural environments. *Ecological Economics, 65*(3), 559-568. doi:10.1016/j.ecolecon.2007.08.006

Castro-Sanguino, C., Ortiz, J. C., Thompson, A., Wolff, N. H., Ferrari, R., Robson, B., . . . Uthicke, S. (2021). Reef state and performance as indicators of cumulative impacts on coral reefs. *Ecological Indicators, 123*, 107335. doi:https://doi.org/10.1016/j.ecolind.2020.107335

Claar, D. C., Szostek, L., McDevitt-Irwin, J. M., Schanze, J. J., & Baum, J. K. (2018). Global patterns and impacts of El Niño events on coral reefs: A meta-analysis. *PLoS ONE, 13*(2), e0190957. doi:10.1371/journal.pone.0190957

Conand, C. (1983). *Abondance, cycle sexuel et relations biométriques de l'étoile Acanthaster planci en Nouvelle-Calédonie*. Retrieved from Nouméa, New Caledonia:

Condie, S. A., Anthony, K. R. N., Babcock, R. C., Baird, M. E., Beeden, R., Fletcher, C. S., . . . Westcott, D. A. (in review). Large-scale interventions may delay decline of the Great Barrier Reef. *Royal Society Open Science*.

Condie, S. A., Plagányi, É. E., Morello, E. B., Hock, K., & Beeden, R. (2018). Great Barrier Reef recovery through multiple interventions. *Conservation Biology, 32*(6), 1356-1367. doi:https://doi.org/10.1111/cobi.13161

Cowan, Z.-L., Dworjanyn, S. A., Caballes, C. F., & Pratchett, M. (2016). Benthic Predators Influence Microhabitat Preferences and Settlement Success of Crown-of-Thorns Starfish (Acanthaster cf. solaris). *Diversity, 8*(4), 27. Retrieved from https://www.mdpi.com/1424-2818/8/4/27

Cowan, Z.-L., Pratchett, M., Messmer, V., & Ling, S. (2017). Known Predators of Crown-of-Thorns Starfish (Acanthaster spp.) and Their Role in Mitigating, If Not Preventing, Population Outbreaks. *Diversity, 9*(1), 7. Retrieved from https://www.mdpi.com/1424-2818/9/1/7

Dana, T. F. (1970). Acanthaster: A Rarity in the Past? *Science, 169*(3948), 894. doi:10.1126/science.169.3948.894

De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences, 109*(44), 17995-17999. doi:10.1073/pnas.1208909109

De'ath, G., & Moran, P. J. (1998). Factors affecting the behaviour of crown-of-thorns starfish (Acanthaster planci L.) on the Great Barrier Reef:: 2: Feeding preferences. *Journal of Experimental Marine Biology and Ecology, 220*(1), 107-126. doi:http://dx.doi.org/10.1016/S0022-0981(97)00100-7

Deaker, D. J., Agüera, A., Lin, H.-A., Lawson, C., Budden, C., Dworjanyn, S. A., . . . Byrne, M. (2020). The hidden army: corallivorous crown-of-thorns seastars can spend years as herbivorous juveniles. *Biology Letters, 16*(4), 20190849. doi:doi:10.1098/rsbl.2019.0849

Dixon, I. (1996). Renewed crown-of-thorns threat. In: Pergamon.

Fabricius, K. E., De'ath, G., Puotinen, M. L., Done, T., Cooper, T. F., & Burgess, S. C. (2008). Disturbance gradients on inshore and offshore coral reefs caused by a severe tropical cyclone. *Limnology and Oceanography, 53*(2), 690-704. doi:https://doi.org/10.4319/lo.2008.53.2.0690

Fabricius, K. E., Okaji, K., & De'ath, G. (2010). Three lines of evidence to link outbreaks of the crown-of-thorns seastar Acanthaster planci to the release of larval food limitation. *Coral Reefs, 29*(3), 593-605. doi:10.1007/s00338-010-0628-z

Firth, S., & McKenzie, C. (2015). *Crown-of-thorns starfish (COTS) control program : Voyage data - Catch per Unit of Effort (CPUE), Eradicated COTS size and coral cover from July 2013 - Jan 2015 (AMPTO)*. Retrieved from: http://eatlas.org.au/geonetwork/srv/eng/metadata.show?uuid=fe100cb3-9b29-4e6b-a8e1-0434631064fa&currTab=complete

Fisk, D. A., & Power, M. C. (1999). *Development of cost-effective control strategies for crown-of-thorns starfish*: CRC Reef Research Centre.

Fletcher, C. S., Bonin, M. C., & Westcott, D. A. (2020). *An ecologically-based operational strategy for COTS Control: Integrated decision making from the site to the regional scale*. Retrieved from Cairns:

Fletcher, C. S., & Westcott, D. A. (2013). Dispersal and the design of effective management strategies for plant invasions: matching scales for success. *Ecological Applications, 23*(8), 1881-1892. doi:10.1890/12-2059.1

Fletcher, C. S., & Westcott, D. A. (2016). *Strategies for Surveillance and Control: Using Crown-of-Thorns Starfish management program data to optimally distribute management resources between surveillance and control. Report to the National Environmental Science Programme. Reef and Rainforest Research Centre Limited*. Retrieved from Cairns:

Fletcher, C. S., Westcott, D. A., Murphy, H. T., Grice, A. C., & Clarkson, J. R. (2015). Managing breaches of containment and eradication of invasive plant populations. *Journal of Applied Ecology, 52*(1), 59-68. doi:10.1111/1365-2664.12361

Gårdmark, A., Lindegren, M., Neuenfeldt, S., Blenckner, T., Heikinheimo, O., Müller-Karulis, B., . . . Möllmann, C. (2013). Biological ensemble modeling to evaluate potential futures of living marine resources. *Ecological Applications, 23*(4), 742-754. doi:https://doi.org/10.1890/12-0267.1

Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-Term Region-Wide Declines in Caribbean Corals. *Science, 301*(5635), 958-960. doi:10.1126/science.1086050

GBRMPA. (2020). *Integrated pest management operations manual for crown-of-thorns starfish control program vessels*. Townsville: Great Barrier Reef Marine Park Authority

Gladstone, W. (1993). *The history of crown-of-thorns starfish controls on the Great Barrier Reef and an assessment of future needs for controls*. Paper presented at the The Possible cause and consequences of outbreaks of the crown-ofthorns starfish. , Proceedings of a workshop held in Townsville, Queensland, Australia.

Hock, K., Doropoulos, C., Gorton, R., Condie, S. A., & Mumby, P. J. (2019). Split spawning increases robustness of coral larval supply and inter-reef connectivity. *Nature Communications, 10*(1), 3463. doi:10.1038/s41467-019-11367-7

Hock, K., Wolff, N. H., Beeden, R., Hoey, J., Condie, S. A., Anthony, K. R. N., . . . Mumby, P. J. (2016). Controlling range expansion in habitat networks by adaptively targeting source populations. *Conservation Biology, 30*(4), 856-866. doi:https://doi.org/10.1111/cobi.12665

Hock, K., Wolff, N. H., Condie, S. A., Anthony, K. R. N., & Mumby, P. J. (2014). Connectivity networks reveal the risks of crown-of-thorns starfish outbreaks on the Great Barrier Reef. *Journal of Applied Ecology, 51*(5), 1188-1196. doi:https://doi.org/10.1111/1365-2664.12320

Hock, K., Wolff, N. H., Ortiz, J. C., Condie, S. A., Anthony, K. R. N., Blackwell, P. G., & Mumby, P. J. (2017). Connectivity and systemic resilience of the Great Barrier Reef. *PLoS Biology, 15*(11), e2003355. doi:10.1371/journal.pbio.2003355

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. *Mar. Freshwater Res., 50*(8), 839. doi:10.1071/mf99078

Hughes, T. P. (2003). Climate Change, Human Impacts, and the Resilience of Coral Reefs. *Science, 301*(5635), 929-933. doi:10.1126/science.1085046

Hughes, T. P., Anderson, K. D., Connolly, S. R., Heron, S. F., Kerry, J. T., Lough, J. M., . . . Wilson, S. K. (2018). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science, 359*(6371), 80-83. doi:10.1126/science.aan8048

Hughes, T. P., Kerry, J. T., & Simpson, T. (2018). Large-scale bleaching of corals on the Great Barrier Reef. *Ecology, 99*(2), 501-501. doi:10.1002/ecy.2092

Johnson, C. R., Sutton, D. C., Olson, R. R., & Giddins, R. (1991). Settlement of crown-of-thorns starfish: role of bacteria on surfaces of coralline algae and a hypothesis for deepwater recruitment. *Marine Ecology Progress Series, 71*(2), 143-162. Retrieved from http://www.jstor.org/stable/24817386

Johnson, D., Moran, P., & Driml, S. (1990). Evaluation of a crown-of-thorns starfish (Acanthaster planci) control program at Grub Reef (central Great Barrier Reef). *Coral Reefs, 9*(3), 167-171.

Keesing, J., & Halford, A. (1992). Importance of postsettlement processes for the population dynamics of <I>Acanthaster planci</I> (L. ). *Marine and Freshwater Research, 43*(3), 635-651. doi:http://dx.doi.org/10.1071/MF9920635

Keesing, J. K., Wiedermeyer, W. L., Okaji, K., Halford, A. R., Hall, K. C., & Cartwright, C. M. (1996). Mortality rates of juvenile starfish Acanthaster planci and Nardoa spp. measured on the Great Barrier Reef, Australia and in Okinawa, Japan. *Oceanologica Acta, 19*, 441–448.

Kenchington, R. (1977). Growth and recruitment of Acanthaster planci (L.) on the great barrier reef. *Biological Conservation, 11*(2), 103-118. doi:10.1016/0006-3207(77)90032-5

Kenchington, R., & Kelleher, G. (1992). Crown-of-thorns starfish management conundrums. *Coral Reefs, 11*(2), 53-56. doi:10.1007/bf00357422

Kenchington, R. A., & Pearson, R. (1982). *Crown-of-Thorns Starfish on the Great Barrier Reef: a situation report*. Paper presented at the Proceedings of the 4th International Coral Reef Symposium, Manila, Philippines.

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

Liaw, A., & Wiener, M. (2002). Classification and regression by randomForest. *R news, 2*(3), 18-22.

Lough, J. M., Anderson, K. D., & Hughes, T. P. (2018). Increasing thermal stress for tropical coral reefs: 1871–2017. *Scientific Reports, 8*(1), 6079. doi:10.1038/s41598-018-24530-9

Lucas, J. S. (1975). Environmental influences on the early development of Acanthaster planci (L.). In A. Canberra (Ed.), *Crown-of-Thorns Starfish Seminar Proceedings, Brisbane*. Australian Government Publishing Service: 109–121.

Lucas, J. S. (1982). Quantitative studies of feeding and nutrition during larval development of the coral reef asteroid Acanthaster planci (L.). *Journal of Experimental Marine Biology and Ecology, 65*(2), 173-193. doi:http://dx.doi.org/10.1016/0022-0981(82)90043-0

Lucas, J. S. (1984). Growth, maturation and effects of diet in *Acanthasterplanci* (L.) (Asteroidea) and hybrids reared in the laboratory. *Journal of Experimental Marine Biology and Ecology, 79*(2), 129-147. doi:10.1016/0022-0981(84)90214-4

MacNeil, M. A., Mellin, C., Pratchett, M. S., Hoey, J., Anthony, K. R. N., Cheal, A. J., . . . Fonnesbeck, C. J. (2016). Joint estimation of crown of thorns (Acanthaster planci) densities on the Great Barrier Reef. *PeerJ, 4*, e2310. doi:10.7717/peerj.2310

Marshall, P. A., & Baird, A. H. (2000). Bleaching of corals on the Great Barrier Reef: differential susceptibilities among taxa. *Coral Reefs, 19*(2), 155-163. doi:10.1007/s003380000086

Mason, R. A. B., Bozec, Y.-M., Hock, K., & Mumby, P. J. (2020). *Climate change trajectories and management intervention benefits for the Great Barrier Reef. Report prepared for the Office of the Great Barrier Reef.* Retrieved from Australia:

Mellin, C., Aaron MacNeil, M., Cheal, A. J., Emslie, M. J., & Julian Caley, M. (2016). Marine protected areas increase resilience among coral reef communities. *Ecology Letters, 19*(6), 629-637. doi:https://doi.org/10.1111/ele.12598

Moran, P. J. (1986). The Acanthaster phenomenon. In H. Barnes & M. Barnes (Eds.), *Oceanography and Marine Biology, An Annual Review*. 379–480: Aberdeen University Press.

Moran, P. J., Bradbury, R. H., & Reichelt, R. E. (1988). Distribution of recent outbreaks of the crown-of-thorns starfish (Acanthaster planci) along the Great Barrier Reef: 1985?1986. *Coral Reefs, 7*(3), 125-137. doi:10.1007/bf00300972

Morello, E. B., Plagányi, É. E., Babcock, R. C., Sweatman, H., Hillary, R., & Punt, A. E. (2014). Model to manage and reduce crown-of-thorns starfish outbreaks. *Marine Ecology Progress Series, 512*, 167-183. doi:10.3354/meps10858

Olson, R. R. (1987). In situ culturing as a test of the larval starvation hypothesis for the crown-of-thorns starfish, Acanthaster planci. *Limnol. Oceangr., 32*(4), 895-904. doi:10.4319/lo.1987.32.4.0895

Ormond, R. F. G., & Campbell, A. C. (1971). Observations on Acanthaster planci and other coral reef echinoderms in the Sudanese Red Sea. *Symposia of the Zoological Society of London, 28*, 433–454.

Osborne, K., Dolman, A. M., Burgess, S. C., & Johns, K. A. (2011). Disturbance and the Dynamics of Coral Cover on the Great Barrier Reef (1995–2009). *PLoS ONE, 6*(3), e17516. doi:10.1371/journal.pone.0017516

Pan, M., Hilomen, V., & Palomares, M. L. D. (2010). Size structure of Acanthaster planci populations in Tubbataha Reefs Natural Parks, Sulu Sea, Philippines. In M. L. D. Palomares & D. Pauly (Eds.), *Marine Biodiversity of Southeast Asian and Adjacent Seas* (pp. 18(13)). Vancouver, Canada: University of British Columbia: Fisheries Centre Research Reports.

Pearson, R. G. (1981). Recovery and Recolonization of Coral Reefs. *Marine Ecology Progress Series, 4*, 105-122. doi:10.3354/meps004105

Pearson, R. G., & Endean, R. (1969). A preliminary study of the coral predator Acanthaster planci (L.) (Asteroidea) on the Great Barrier Reef. *Fisheries Notes, Queensland Department of Harbours and Marine, 3*, 27–55.

Plaganyi, E., Babcock, R., Morello, E. B., Zhou, S., Rochester, W., Ellis, N., & Punt, A. (2014). *An integrated overview of the causes of crown-of-thorns starfish (COTS) outbreaks, and scenarios for assessing the efficacy of different combinations of management and mitigation measures, Draft Report*. Retrieved from Australia:

Pratchett, M. S. (1999). An infectious disease in crown-of-thorns starfish on the Great Barrier Reef. *Coral Reefs, 18*(3), 272-272. doi:10.1007/s003380050192

Pratchett, M. S. (2005). Dynamics of an outbreak population of Acanthaster planci at Lizard Island, northern Great Barrier Reef (1995–1999). *Coral Reefs, 24*(3), 453-462. doi:10.1007/s00338-005-0006-4

Pratchett, M. S. (2010). Changes in coral assemblages during an outbreak of Acanthaster planci at Lizard Island, northern Great Barrier Reef (1995–1999). *Coral Reefs, 29*(3), 717-725. doi:10.1007/s00338-010-0602-9

Pratchett, M. S., Caballes, C. F., Rivera-Posada, J. A., & Sweatman, H. P. A. (2014). Limits to Understanding and Managing Outbreaks of Crown-of-Thorns Starfish (*Acanthaster* spp.). *Oceanography and Marine Biology: An Annual Review, 52*, 133-200. doi:doi:10.1201/b17143-4

Pratchett, M. S., Caballes, C. F., Wilmes, J. C., Matthews, S., Mellin, C., Sweatman, H. P. A., . . . Uthicke, S. (2017). Thirty Years of Research on Crown-of-Thorns Starfish (1986–2016): Scientific Advances and Emerging Opportunities. *Diversity, 9*(4), 41. Retrieved from https://www.mdpi.com/1424-2818/9/4/41

Pratchett, M. S., Cowan, Z.-L., Nadler, L. E., Caballes, C. F., Hoey, A. S., Messmer, V., . . . Ling, S. D. (2017). Body size and substrate type modulate movement by the western Pacific crown-of-thorns starfish, Acanthaster solaris. *PLoS ONE, 12*(9). doi:10.1371/journal.pone.0180805

Price, M. (2018). New starfish-fighting fleet on the horizon [Press release]. Retrieved from https://web.archive.org/web/20180911124438/https://www.environment.gov.au/minister/price/media-releases/mr20180613.html

Puotinen, M., Maynard, J. A., Beeden, R., Radford, B., & Williams, G. J. (2016). A robust operational model for predicting where tropical cyclone waves damage coral reefs. *Scientific Reports, 6*(1), 26009. doi:10.1038/srep26009

R Core Team. (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing. Vienna, Austria. Retrieved from https://www.R-project.org/

Raymond, R. (1986). *Starfish Wars: Coral Death and the Crown-of-Thorns*. South Yarra, Australia: Macmillan.

Reichelt, R. E., Bradbury, R. H., & Moran, P. J. (1990). Distribution of Acanthaster planci outbreaks on the Great Barrier Reef between 1966 and 1989. *Coral Reefs, 9*(3), 97-103. doi:10.1007/BF00258219

Rivera-Posada, J., & Prattchet, M. (2012). *A review of existing control efforts for Acanthaster planci; limitations to successes, Report to the Department of Sustainability, Environment, Water, Population & Communities,*. Townsville, June 5 2012

Roughgarden, J., Gaines, S., & Possingham, H. (1988). Recruitment dynamics in complex life cycles. *Science, 241*(4872), 1460-1466. doi:10.1126/science.11538249

Sharov, A. A., & Liebhold, A. M. (1998). Bioeconomics of managing the spread of exotic pest species with barrier zones. *Ecological Applications, 8*(3), 833-845. doi:10.1890/1051-0761(1998)008[0833:bomtso]2.0.co;2

Sharov, A. A., & Liebhold, A. M. (1998). Model of slowing the spread of gypsy moth (Lepidoptera: Lymantriidae) with a barrier zone. *Ecological Applications, 8*(4), 1170-1179.

Sharov, A. A., Liebhold, A. M., & Roberts, E. A. (1998). Optimizing the use of barrier zones to slow the spread of gypsy moth (Lepidoptera: Lymantriidae) populations in North America. *Journal of Economic Entomology, 91*(1), 165-174.

Sigl, R., Steibl, S., & Laforsch, C. (2016). The role of vision for navigation in the crown-of-thorns seastar, Acanthaster planci. *Scientific Reports, 6*(1), 30834. doi:10.1038/srep30834

Steven, A. D. L., Baird, M. E., Brinkman, R., Car, N. J., Cox, S. J., Herzfeld, M., . . . Yu, J. (2019). eReefs: An operational information system for managing the Great Barrier Reef. *Journal of Operational Oceanography, 12*(sup2), S12-S28. doi:10.1080/1755876X.2019.1650589

Stump, R. J. W. (1996). *An investigation of the methods to describe the population dynamics of Acanthaster planci (L.) around Lizard Island, northern Cairns Section, GBR Technical report no. 10*. Retrieved from Townsville, Australia:

Sweatman, H. (2008). No-take reserves protect coral reefs from predatory starfish. *Current Biology, 18*(14), R598-R599. doi:http://dx.doi.org/10.1016/j.cub.2008.05.033

Treml, E. A., Halpin, P. N., Urban, D. L., & Pratson, L. F. (2008). Modeling population connectivity by ocean currents, a graph-theoretic approach for marine conservation. *Landscape Ecology, 23*(1), 19-36. doi:10.1007/s10980-007-9138-y

Uthicke, S., Schaffelke, B., & Byrne, M. (2009). A boom–bust phylum? Ecological and evolutionary consequences of density variations in echinoderms. *Ecological Monographs, 79*(1), 3-24. doi:https://doi.org/10.1890/07-2136.1

Vanhatalo, J., Hosack, G. R., & Sweatman, H. (2017). Spatiotemporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. *Journal of Applied Ecology, 54*(1), 188-197. doi:https://doi.org/10.1111/1365-2664.12710

Vercelloni, J., Caley, M. J., & Mengersen, K. (2017). Crown-of-thorns starfish undermine the resilience of coral populations on the Great Barrier Reef. *Global Ecology and Biogeography, 26*(7), 846-853. doi:https://doi.org/10.1111/geb.12590

Vine, P. J. (1973). Crown of thorns (Acanthaster planci) plagues: the natural causes theory. *Atoll Research Bulletin, 166*, 1-10. doi:10.5479/si.00775630.166.1

Walsh, R., & et al. (1971). *Report of the Committee on the Problem of the Crown-of-thorns Starfish (Acanthaster Planci)*. Retrieved from Canberra, Australia:

Westcott, D. A., & Fletcher, C. S. (2018). *How Effective Are Management Responses In Controlling Crown-of-Thorns Starfish and their Impacts On The Great Barrier Reef? Report to the National Environmental Science Program. Reef and Rainforest Research Centre Limited*. Retrieved from Cairns:

Westcott, D. A., Fletcher, C. S., Babcock, R., & Plaganyi-Lloyd, E. (2016). *A Strategy to Link Research and Management of Crown-of-Thorns Starfish on the Great Barrier Reef: An Integrated Pest Management Approach, Report to the National Environmental Science Programme*. Retrieved from

Westcott, D. A., Fletcher, C. S., Gladish, D. W., MacDonald, S., & Condie, S. (2021). *Integrated Pest Management Crown-of-Thorns Starfish Control Program on the Great Barrier Reef: Current Performance and Future Potential. Report to the National Environmental Science Program.* Retrieved from Cairns, Australia:

Westcott, D. A., Fletcher, C. S., Kroon, F. J., Babcock, R. C., Plagányi, E. E., Pratchett, M. S., & Bonin, M. C. (2020). Relative efficacy of three approaches to mitigate Crown-of-Thorns Starfish outbreaks on Australia's Great Barrier Reef. *Scientific Reports, 10*(1), 12594. doi:10.1038/s41598-020-69466-1

Wolfe, K., Graba-Landry, A., Dworjanyn, S. A., & Byrne, M. (2017). Superstars: Assessing nutrient thresholds for enhanced larval success of Acanthaster planci, a review of the evidence. *Marine Pollution Bulletin, 116*(1), 307-314. doi:https://doi.org/10.1016/j.marpolbul.2016.12.079

Wolff, N. H., Mumby, P. J., Devlin, M., & Anthony, K. R. N. (2018). Vulnerability of the Great Barrier Reef to climate change and local pressures. *Global Change Biology, 24*(5), 1978-1991. doi:https://doi.org/10.1111/gcb.14043

Wolff, N. H., Wong, A., Vitolo, R., Stolberg, K., Anthony, K. R., & Mumby, P. J. (2016). Temporal clustering of tropical cyclones on the Great Barrier Reef and its ecological importance. *Coral Reefs, 35*(2), 613-623.

Wooldridge, S. A., & Brodie, J. E. (2015). Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. *Marine Pollution Bulletin, 101*(2), 805-815. doi:http://dx.doi.org/10.1016/j.marpolbul.2015.08.049

Yamaguchi, M. (1973). Early Life Histories of Coral Reef Asteroids, with Special Reference to *Acanthaster planci* (L.). In O. A. Jones & R. Endean (Eds.), *Biology and Geology of Coral Reefs* (pp. 369-387). New York: Academic Press.

Yamaguchi, M. (1974). Growth of juvenile Acanthaster planci (L.) in the laboratory. *Pacific Science, 28*, 123–138.

Yamaguchi, M. (1986). Acanthaster planci infestations of reefs and coral assemblages in Japan: a retrospective analysis of control efforts. *Coral Reefs, 5*(1), 23-30. doi:10.1007/bf00302168

Zann, L., Brodie, J., Berryman, C., & Naqasima, M. (1987). Recruitment, ecology, growth and behavior of juvenile Acanthaster planci (L.) (Echinodermata: Asteroidea). *Bulletin of Marine Science, 41*, 561–575.

Zann, L., & Weaver, K. (1988). *An evaluation of crown-of-thorns starfish control programs undertaken on the Great Barrier Reef.* Paper presented at the Proc. 6th int. coral Reef Symp.

Reef & Rainforest RESEARCH CENTRE

www.nesptropical.edu.au