COTS Control Innovation Program

TECHNICAL REPORT

Early detection of renewed population irruptions of Pacific crown-of-thorns starfish (*Acanthaster cf. solaris*) on Australia's Great Barrier Reef

Morgan S. Pratchett, Peter C. Doll, Josie F. Chandler, Jason R. Doyle,
Sven Uthicke, Alexia Dubuc, and Ciemon F. Caballes

Early detection of renewed population irruptions of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on Australia's Great Barrier Reef

Morgan S. Pratchett[1], Peter C. Doll[1], Josie F. Chandler[1], Jason R. Doyle[2], Sven Uthicke[2], Alexia Dubuc[1], and Ciemon F. Caballes[3]

1. College of Science and Engineering, James Cook University
2. Australian Institute of Marine Science
3. University of Guam Marine Laboratory

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

Inquiries should be addressed to:

Morgan S. Pratchett
College of Science and Engineering, James Cook University
morgan.pratchett@jcu.edu.au

This report should be cited as

Pratchett MS, Doll PC, Chandler JF, Doyle JR, Uthicke S, Dubuc A, Caballes CF (2025) *Early detection of renewed population irruptions of Pacific crown-of-thorns starfish (*Acanthaster *cf.* solaris) *on Australia's Great Barrier Reef*. A report to the Australian Government by the COTS Control Innovation Program (53 pp).

Funding Acknowledgement

The COTS Control Innovation Program aims to accelerate the development of innovative surveillance and control methods to manage outbreaks of coral-eating starfish on the Great Barrier Reef. The Program is a collaboration between the Great Barrier Reef Foundation, Australian Institute of Marine Science, Commonwealth Scientific and Industrial Research Organisation, James Cook University and The University of Queensland. The Program is funded by the partnership between the Australian Government's Reef Trust and the Great Barrier Reef Foundation.

Traditional Owner Acknowledgement

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

Disclaimer

Copyright

Contents

List of Figures

List of Tables

Acronynms and Abbreviations

AICc	Akaike Information Criteria - corrected
AIMS	Australian Institute of Marine Science
COTS	Crown-of-thorns starfish
CCIP	COTS Control Innovation Program
eDNA	Environmental DNA
GBR	Great Barrier Reef
GBRMP	GBR Marine Park
GLM	Generalised Linear Model
GLMM	Generalised Linear Mixed Model
GPS	Global Positioning System
JCU	James Cook University
LTMP	Long-Term Monitoring Program
PIT	Point Intercept Transects
RNTBC	Registered Native Title Body Corporate
SALAD	Scooter-assisted large area diver-based (SALAD) surveys
TO	Traditional Owner
TUMRA	Traditional Use of Marine Resources Agreement

EXECUTIVE SUMMARY

Recurrent population irruptions of the Pacific crown-of-thorns starfish (COTS; *Acanthaster* cf. *solaris*) remain one of the foremost causes of coral mortality on Australia's Great Barrer Reef (GBR), contributing to substantial declines in coral cover and reef health. Preventing or minimising coral loss due to current and future population irruptions of COTS is critical for improving the status and outlook of coral reef ecosystems across the GBR. Establishing when, where, and why these population irruptions start is fundamental to effective large-scale and long-term management. Previous population irruptions of COTS on the GBR are purported to have started on reefs between Lizard Island (14.6°S) and Cairns (17°S), an area commonly referred to as the *initiation area*. However, in previous outbreaks there were detectable increases in the abundance of adult COTS in the far northern GBR well ahead of similar reports for reefs within the putative *initiation area* (e.g. Lizard Island). This study used new and effective sampling methods to assess inter-annual variation in the abundance and size of COTS across the northern GBR from 2021–2024, testing for increasing densities of COTS that might represent the precursor of impending population irruptions.

A key limitation in the capacity to effectively survey COTS and identify initial increases in the local abundance is their limited detectability. Critically, COTS tend to be highly cryptic, especially at smaller size classes and during daylight hours. The local occurrence of COTS is often apparent based mainly on conspicuous feeding scars, rather than sighting or recording individual COTS. Careful searching within the reef matrix in the immediate vicinity of unequivocal feeding scars often leads to detection of relevant COTS, though this is not possible during large-scale or rapid surveys, which have traditionally been achieved using manta-tow methods. In this study, we used scooter-assisted large area diver-based (SALAD) surveys to substantially increase the spatial extent of visual surveys undertaken by SCUBA divers, while allowing for the opportunity to stop and search for COTS within complex reef habitats especially when feeding scars were observed.

A total of 552 SALAD surveys were conducted across 20 reefs in 4 distinct regions, encompassing a combined survey area of 277.54 hectares. A total of 1,161 COTS, as well as a further 1,142 distinct sets of feeding scars, were recorded across all SALAD surveys, resulting in an average inferred density (including sets of scars) of 11.64 COTS.ha^{-1} (±0.67 SE). Inferred densities were higher in the Cape Grenville region (17.45 COTS.ha^{-1} ±1.47 SE) and Lizard Island region (14.01 COTS.ha^{-1} ±1.17 SE), compared to the Princess Charlotte Bay region (8.52 COTS.ha^{-1} ±1.53 SE) and the Cairns region (5.15 COTS.ha^{-1} ±0.50 SE). COTS densities increased from 2021 to 2024 in the Lizard Island region, but were relatively stable in the Cape Grenville and Princess Charlotte Bay regions, and declined throughout this study in the Cairns region.

Aside from elevated densities of COTS recorded in the Cape Grenville and Lizard Island regions, the mean size (diameter) of COTS recorded in the Cape Grenville region (404.8 mm ±4.05 SE, n = 325) and the Lizard Island region (392.5 mm ±4.18 SE n = 496) was substantially higher than recorded in the Princess Charlotte Bay region (247.5 mm ±9.53 SE, n = 101) and Cairns region (289.8 mm ±13.20 SE, n= 47). Larger COTS (> 50 cm diameter) were recorded exclusively in the Cape Grenville and Lizard Island regions.

COTS detectability (estimated based on the proportion of COTS sighted versus those that were not detected despite apparent sets of feeding scars) averaged 47.25% across all SALAD surveys where COTS or feeding scars were recorded (n = 518 surveys). Detectability was much higher in the Cape Grenville region (59.46% ±2.96 SE) and the Lizard Island region (49.85% ±2.30 SE), compared to the Princess Charlotte Bay region (41.01% ±4.91 SE) and the Cairns region (36.85% ±3.21 SE). These differences appear to reflect regional differences in the size of COTS, whereas there was no relationship between detectability and COTS densities.

Diver-independent analyses of COTS abundance based on eDNA sampling largely complemented variation in local abundance of COTS established using SALAD surveys. In particular, a very high proportion of replicate water samples from sites sampled in the Cape Grenville regions had positive detections of eDNA for COTS (approaching 1.0), which is also where the highest densities of COTS were recorded (up to 40.32 COTS.ha^{-1}). Overall, there was a strong and positive (adjusted $r^2 = 0.52$) relationship between recorded density from SALAD surveys and proportion of eDNA samples positive for COTS, demonstrating utility of both these methods for detecting low densities of COTS and the early initiation of population irruptions.

This study provides unprecedented insights into the spatiotemporal patterns of COTS abundance during the apparent initiation of renewed outbreaks. Critically, there have been substantial increases in densities of COTS recorded at Lizard Island between 2021 and2024, with average reef-wide densities now exceeding 15 COTS.ha^{-1}. These data support the notion that renewed population irruptions of COTS have commenced in the northern GBR, representing the fifth documented episode of population irruptions since the 1960s. Importantly, however, there were detectable increases in the abundance of adult COTS in the far northern GBR well ahead of documented increases at reefs within the putative *initiation area* (e.g. Lizard Island). Together with new hydrodynamic models that demonstrate the potential southward flow in the far northern GBR and corresponding dispersal of larval propagules during summer months, these results challenge the prevailing paradigms regarding the underlying cause(s) of population irruptions on the GBR and necessitate a re-thinking of appropriate management responses.

Recent and extensive research into putative causes of population irruptions of COTS on the GBR has focused on reefs within the broadly designated *initiation area*, either within the vicinity of Lizard Island or at reefs off Cairns. However, data from this study suggests that population irruptions may originate on reefs in the far northern GBR, and that proliferation of COTS at reefs in the Lizard Island region reflects the secondary accumulation of larvae spawned by burgeoning or expansive populations on reefs to the north. Reefs in the far northern GBR (especially mid shelf reefs north of Cape Grenville) are far removed from anthropogenic and coastal influences, such that the roles of eutrophication from land runoff and/or overfishing of putative fish predators in initiating population irruptions of COTS in this region is tenuous.

1. INTRODUCTION

Coral reef ecosystems are subject to widespread and increasing habitat degradation due to perennial anthropogenic threats (including overfishing, pollution, sedimentation and eutrophication; e.g. Pandolfi et al. 2003), combined with escalating effects of global climate change (Hoegh-Guldberg 1999; Hughes et al. 2003). Reef degradation largely manifests as declines in the abundance of habitat-forming hard corals (order Scleractinia), caused by elevated rates of coral mortality (Mellin et al. 2019), as well as declining growth and replenishment of corals, which constrains recovery (Ortiz et al. 2018). Critically, major disturbances that cause extensive coral mortality are now occurring too frequently on most reefs to allow for full and effective recovery in the intervening period (Pratchett et al. 2014; Hughes et al. 2018).

The foremost cause of significant recent coral mortality is recurrent large-scale coral bleaching and mortality, which is unequivocally linked to anthropogenic global warming (Hoegh-Guldberg 1999; Hughes et al. 2003). However, population irruptions (“plagues”, Vine 1973; “outbreaks”, Weber and Woodhead 1970; or “infestations”, Endean and Stablum 1973) of coral feeding crown-of-thorns starfish (COTS; *Acanthaster* spp.) also represent a significant contributor to coral loss and reef degradation at a broad range of reef locations, especially in the Indo West-Pacific (Pratchett et al. 2024). Ultimately, it is the cumulative effect of natural and anthropogenic disturbances that are contributing to global coral loss and reef degradation (Bellwood et al. 2019), requiring renewed and more effective management to conserve coral reefs and sustain their critical ecosystem services and functions.

1.1 Crown-of-thorns starfish (*Acanthaster* spp.)

Crown-of-thorns starfish (COTS; *Acanthaster* spp.) are the foremost predators of hard corals (order Scleractinia), especially during population irruptions (e.g. Chesher 1969; Reichelt et al. 1990; Kayal et al. 2012). COTS are among the largest and most efficient of all coral predators (Benson 1975; Birkeland 1989), capable of comprehensively removing live tissue from the surface of even highly complex hard corals by everting their stomach through their oral opening and externally digesting coral tissues (Goreau 1964). The feeding capacity of COTS scales with body size (e.g. Keesing and Lucas 1992), such that combined feeding activities of high densities of large starfish rapidly deplete local coral assemblages (Chesher 1969; Kayal et al. 2012). In French Polynesia, for example, high densities of COTS (up to 151,650 ind.km^{-2}) killed > 96% of coral in Moorea between 2005 and 2010 (Kayal et al. 2012). New or renewed population irruptions of COTS remain one of the foremost causes of acute coral loss and have contributed to sustained habitat degradation at many locations throughout the Indo-West Pacific (Trapon et al. 2011; Mellin et al. 2019).

There are at least four distinct species of *Acanthaster* spp. that exhibit population irruptions and can cause significant localised coral loss, which are collectively distributed throughout the Indo-Pacific (Foo et al. 2024; Uthicke et al. 2024a); *Acanthaster benziei* (Wörheide et al. 2022) which occurs in the Red Sea, *Acanthaster planci* (Linnaeus, 1758) which is restricted to the northern Indian Ocean, *Acanthaster mauritiensis* (Loriol 1895) which occurs in the southern Indian Ocean, and *Acanthaster* cf. *solaris* (Schreber 1795) which is broadly distributed throughout the central and western Pacific Ocean. The cause(s) or driver(s) of

COTS population outbreaks are still unresolved (e.g. Pratchett et al. 2014; Babcock et al. 2016a) and may vary among species and regions (Pratchett et al. 2017). It appears, for example, that population irruptions are more intense, and have the greatest impact on coral reef ecosystems in the central and western Pacific (mainly Australia, Japan, New Caledonia and French Polynesia) where *A.* cf. *solaris* occurs (Uthicke et al. 2024a).

1.2 Documenting and detecting population irruptions

Population irruptions of COTS have been reported throughout the Indo-Pacific, from the Red Sea (Ormond et al. 1973) to Hawaii (Kenyon and Aeby 2009). However, most reports of population irruptions are based on qualitative observations of significant and punctuated increases in the appearance or abundance of COTS, rather than rigorous quantitative changes in abundance or threshold densities (Pratchett et al. 2014). Part of the issue in rigorously characterising or distinguishing population irruptions relates to inherent challenges in effectively surveying and recording densities of COTS, especially at relatively low or moderate densities. For the most part, COTS are highly cryptic, especially at low densities, making it very difficult to establish “normal” or baseline densities (Weber and Woodhead 1970; Moran 1986; Fernandes et al. 1990). Conversely, COTS are very conspicuous during major population irruptions (**Figure 1**), but even then, it is likely that many smaller individuals evade detection (MacNeil et al. 2016), leading to underestimates in COTS densities and limited appreciation of population structure.

Establishing patterns of abundance for COTS, and especially the occurrence of population irruptions, necessitates surveying large areas of reef habitat, which has traditionally been achieved using towed-diver (e.g. Kenyon and Aeby 2009) or manta-tow methods (e.g. Vanhatalo et al. 2017). However, such methods are constrained in their capacity to effectively record local COTS densities given the limited proportion of adult COTS that are highly exposed and readily visible from above (Fernandes et al. 1990). Generally, most adult COTS are concealed beneath corals or within the reef matrix, especially during daylight hours (Moran 1986). Accordingly, the local occurrence of COTS is often apparent based on conspicuous feeding scars (e.g. Kayal et al. 2012), rather than sighting or recording individual COTS. Careful searching within the reef matrix in the immediate vicinity of unequivocal feeding scars often leads to detection of relevant COTS, though this is not possible during large-scale or rapid surveys, (e.g. manta tows). Conversely, intensive visual surveys undertaken by autonomous divers (e.g. Pratchett 2005; Kenyon and Aeby 2009; Plass-Johnson et al. 2015) greatly increase the detection of COTS, but are inherently limited in their spatial extent (MacNeil et al. 2016).

The limited detectability of COTS questions the relevance of proposed thresholds for signifying population irruptions (e.g. 15 starfish.ha^{-1}; Moran and De’Ath 1992) or setting management targets (e.g. 3 starfish.ha^{-1}; Rogers et al. 2017), necessitating conversions that account for the specific size structure of COTS and limitations of particularly sampling methods (e.g. Plagányi et al. 2020).

Figure 1. Conspicuous western Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) during population irruptions on Swains Reefs (southern Great Barrier Reef) in February 2021. Photograph: M. Pratchett.

1.3 Recurrent population irruptions on Australia's GBR

There have been four distinct episodes (or *waves*; Babcock et al. 2020) of population irruptions recorded on the GBR since the 1960s (Pratchett et al. 2014), with a latest (fifth) episode now starting in the northern GBR (Chandler et al. 2023; Uthicke et al. 2024b). The first documented instance of elevated densities of COTS on the GBR was in 1959 at Green Island (D. Whitaker, pers. comm. in Pearson and Endean 1969), which resulted in extensive coral loss by 1963 (Barnes 1966). Subsequent surveys (1964–1966) revealed established infestations of adult COTS at Arlington and Batt Reefs (Pearson and Endean 1969). However, there was very limited research and monitoring on reefs to the north of these locations during this period, meaning that earlier or widespread population irruptions may have gone undetected.

Renewed population irruptions in ~1979 were again first noticed at Green Island, where up to 2 million COTS removed > 90% of live coral (Endean 1982). Broadscale surveys in 1980 revealed elevated densities of COTS at several reefs between 14°S and 18°S (Nash and Zell 1981), especially Williamson, U/N 15-043, Green and Arlington, where there were frequently 11–40 starfish recorded per 20-min manta tow. There were also anecdotal reports of recent

COTS activity at Great Detached Reef (11.7ºS) during this period (Kenchington and Pearson 1981).

Reef-wide monitoring (established in 1985) revealed the initiation of renewed outbreaks starting in ~1993 and ~2010 in the vicinity of Lizard Island. Wooldridge and Brodie (2015) maintain that elevated densities of COTS were recorded coincidentally at Michaelmas Cay and Lizard Island in the early 1990s. The earliest detections of elevated COTS densities at the start of successive episodes of population irruptions (in ~1962, ~1979, ~1993, and ~2010) have consistently occurred on reefs between Lizard Island and Green Island in an area that has been referred to as the *initiation area* (Pratchett et al. 2014; Wooldridge and Brodie 2015) encompassing midshelf reefs between Lizard Island (14.6ºS) and Green Island (16.8ºS). Much of the research on putative cause(s) of primary population irruptions (e.g. Cowan et al. 2020; Caballes et al. 2021) has understandably been concentrated in this area.

1.4 Objectives and impact pathway

The purpose of this research was to undertake recurrent annual surveys (2021–2024) to test for changes in abundance and population structure of COTS at select reefs in the Northern and Far Northern sectors of the GBR, to try and establish when and where renewed population irruptions arise. Sampling was partly focused on reefs within the putative initiation area (encompassing midshelf reefs between Cairns and Lizard Island; Pratchett et al. 2014; Wooldridge and Brodie 2015), with further sampling on reefs to the north of this area (Princess Charlotte Bay region and Cape Grenville region), where elevated densities of COTS may precede the emergence or detection of population irruptions within the currently prescribed *initiation area* (e.g. Vanhatalo et al. 2017).

The activities and outputs of this project contribute to the impact pathways related to improved detection and prediction of COTS outbreaks by i) contributing to the ongoing development of novel survey methods for improved detection and monitoring of COTS, especially at low to moderate densities, and ii) improving understanding of the biology and ecology of COTS, especially the patterns and processes involved in the initiation of population irruptions on the GBR (**Figure 2**). Effectively surveying low densities of COTS at a range of locations in the lead up to anticipated population irruptions in 2025–2027 (*sensu* Babcock et al. 2020) was expected to provide unprecedented information on subtle changes in the population dynamics of COTS which is critical for understanding the potential cause(s) or drivers of population irruptions. Moreover, this project is expected to provide benefits for management, whereby early detection of renewed outbreaks would provide opportunities for pre-emptive culling to suppress initial growth of COTS populations and potentially prevent (or contain) population irruptions at the scale of the entire GBR.

The specific objectives of this project were to:

i. Document interannual variation in the size and abundance of COTS across four distinct regions in the Northern and Far Northern sectors of the GBR.

ii. Explore spatiotemporal variation in detectability of COTS, by comparing the proportion of starfish that were or were not sighted within the immediate vicinity of conspicuous sets of feeding scars.

iii. Relate spatiotemporal variation in population size, dynamics and detectability of COTS to local habitat structure and condition, both to assess how habitat condition influences abundance and detectability of COTS and test for localised effects of COTS, based on changing coral cover.

iv. Compare estimates of COTS abundance obtained using diver-based (SALAD surveys) and diver-independent (eDNA) sampling methods especially at low to moderate densities, to establish the utility of these methods for documenting the initiation of population irruptions.

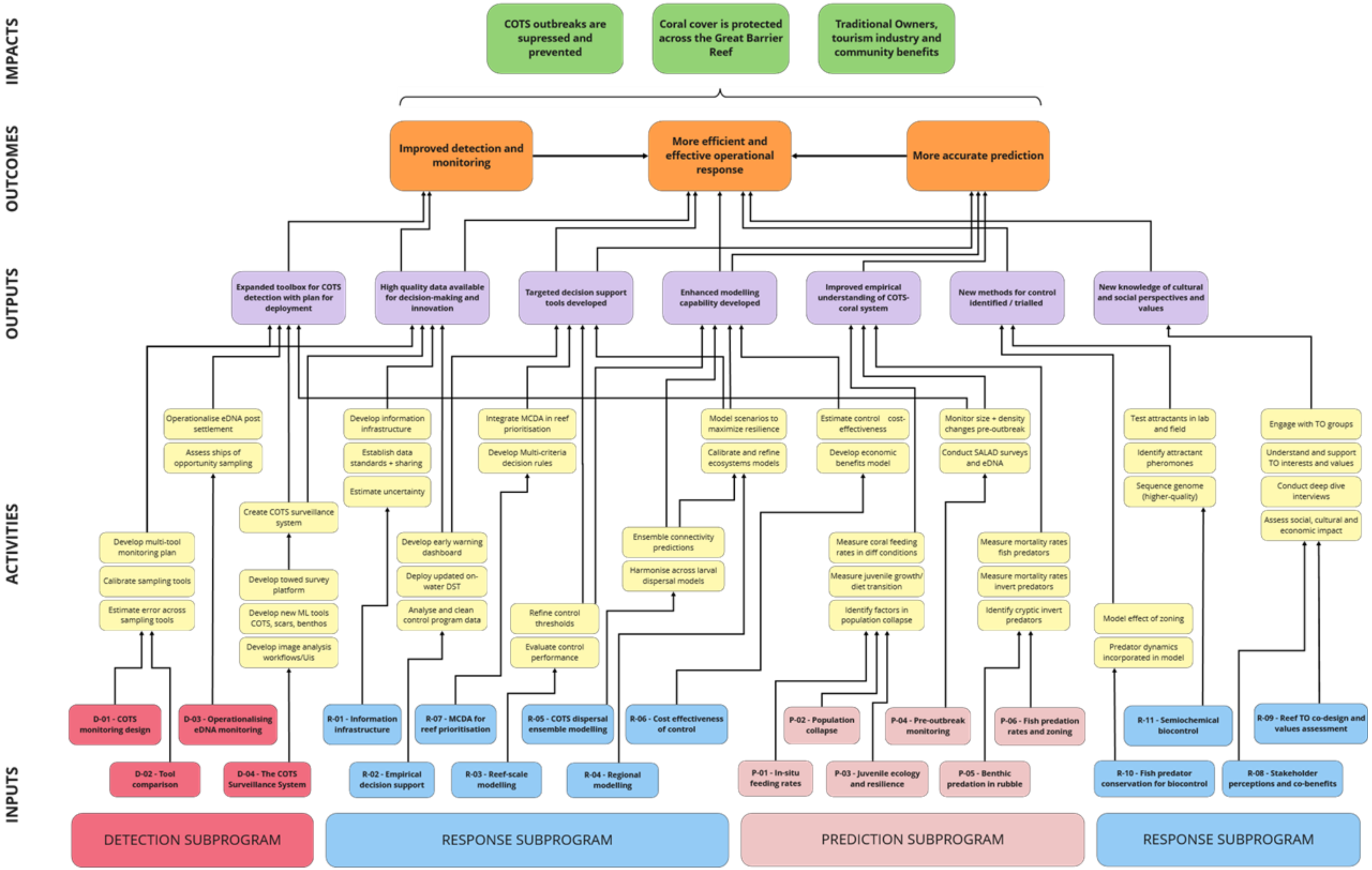

Figure 2. COTS Control Innovation Program (CCIP) program logic showing how this project (P-04) relates to other projects, as well as the overarching outputs, outcomes and impacts

2. METHODS

This study was conducted over three years (2022–2024) but builds upon data collected in 2021 as part of a CCIP early-investment project (Pratchett et al. 2022), as well as complementary sampling initiated in 2019, albeit at a restricted set of reefs and regions (**Table 1**). Sampling was focused on four distinct regions across the Northern (Cairns region and Lizard Island region) and Far Northern sectors (Princess Charlotte Bay and Cape Grenville Region) of the GBR (**Figure 3**), though sampling was also conducted in the Townsville region as part of other CCIP projects (see Section 5). Data will be presented for the full set of years and regions, where relevant.

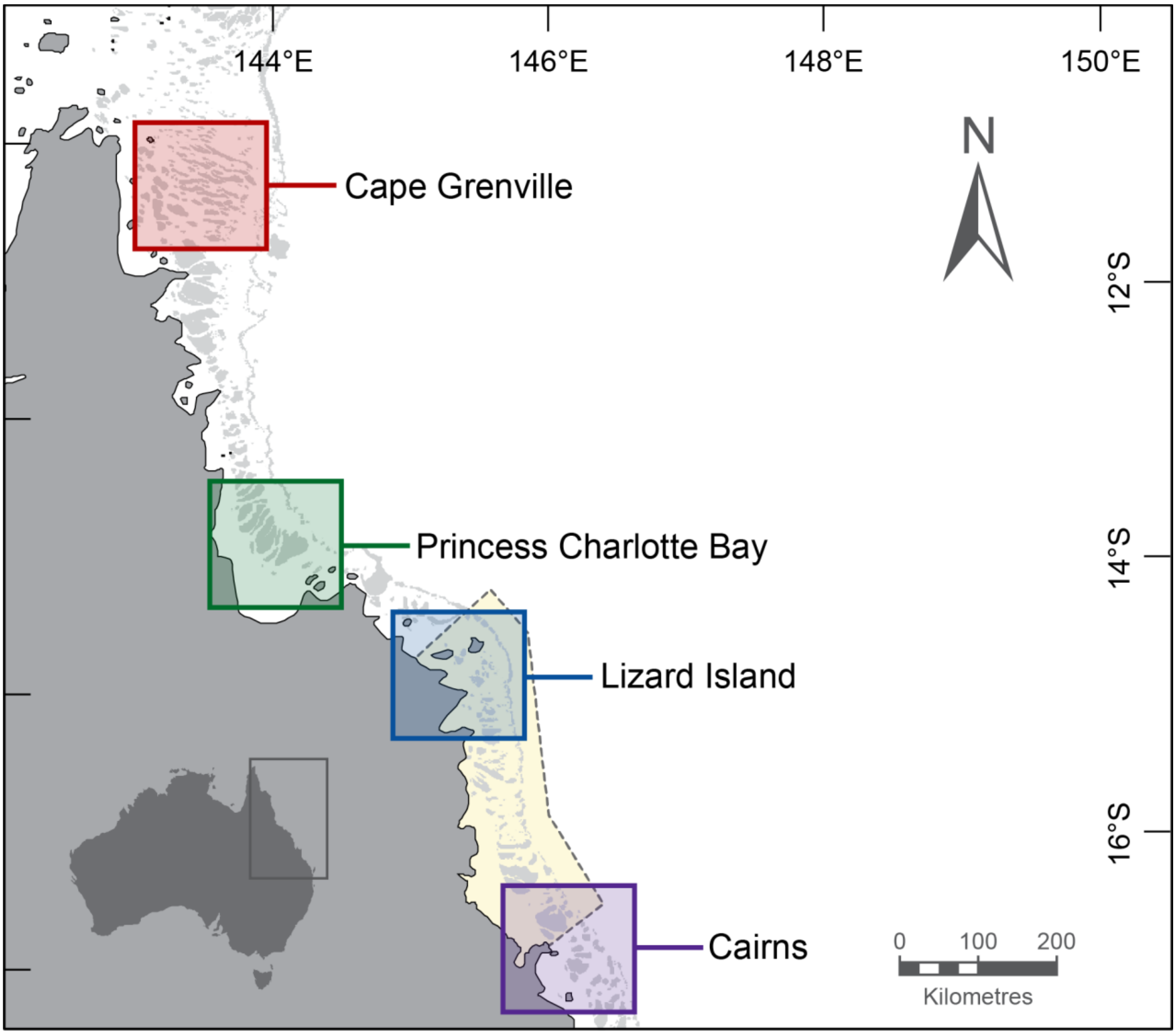

Figure 3. Map of the northern and far northern Great Barrier Reef, showing the putative initiation area (shown in yellow), where population irruptions of western Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) are reported to originate. Labels indicate four distinct regions where sampling was undertaken to test for variation in the size and abundance of crown-of-thorns starfish between 2021 and 2024.

2.1 Scooter-assisted large area diver-based (SALAD) visual surveys

This project used scooter-assisted large area diver-based (SALAD) surveys to survey COTS, following Chandler et al (2023). During each SALAD survey, divers would traverse a section of reef searching for apparent feeding scars and/ or COTS. Divers worked in pairs, but independently surveyed distinct reef zones or depths. For the most part, one diver would survey the shallow reef crest (1–3m depth depending on the tide) while the other diver would simultaneously survey along the reef slope (4–7m depth). The proximity of divers and survey paths was necessarily adjusted depending on visibility and habitat structure. Where practicable, divers used a towed GPS unit (**Figure 4**) to record the specific path taken by each diver. Data from the towed GPS were used mainly to determine the distance travelled (averaging 0.98 km ±0.02 SE), as necessary to establish the total search area and corresponding COTS densities.

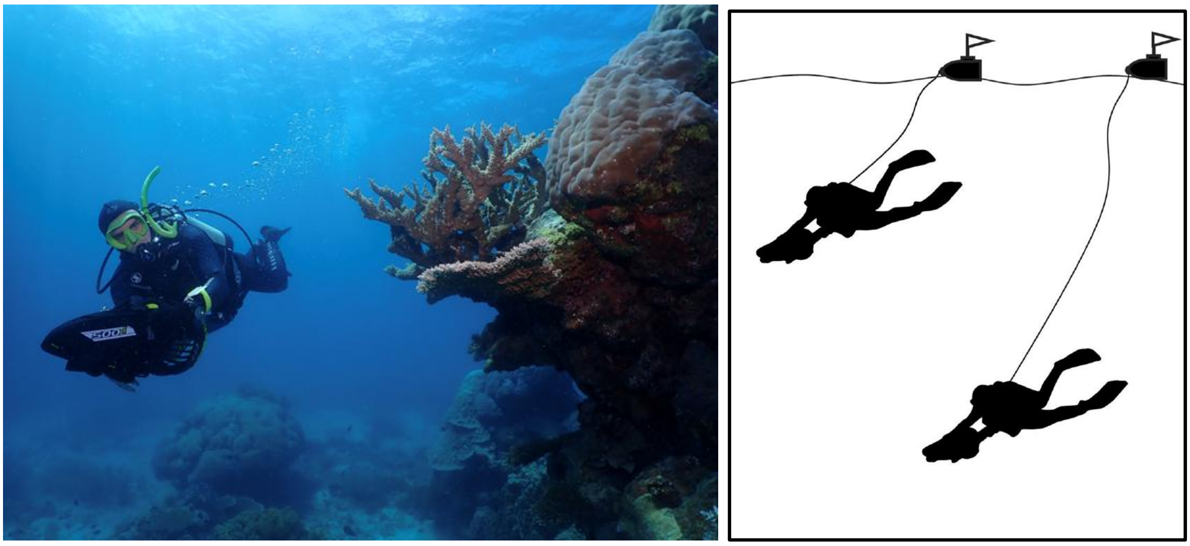

Figure 4. Scooter-assisted large area diver-based (SALAD) surveys used to quantify densities of western Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) across the northern and far northern Great Barrier Reef. Wherever practicable, surveys were conducted at two depths simultaneously, and divers used a towed GPS to record the length of the surveyed path.

The specific location of replicate SALAD surveys conducted in each year at each reef was selected haphazardly from the range of potential areas that were accessible given prevailing conditions. Critically, it was not possible to effectively re-survey the same swaths of reef habitat during successive surveys, and so sites were selected without consideration of previous sampling, intended to provide an independent measure of reef wide COTS densities on each sampling occasion. Sampling was however, largely conducted along northern and western margins of reefs as the predominant conditions encountered were strong winds and persistent swell from the south-east.

During SALAD surveys, most COTS were located only after first sighting apparent feeding scars (see also Kayal et al. 2012). All apparent feeding scars were carefully inspected to rule out tissue loss due to other factors (e.g. coral disease or *Drupella* spp.). If confident that tissue loss was caused by COTS, careful searching was undertaken within the immediate area (up to 5 m in all directions from the most recent feeding scar) to locate the starfish. For every COTS detected, divers recorded i) the size of the starfish (maximum diameter, cm), ii) the time of observation to cross-reference with time-based records of GPS co-ordinates from towed GPS and thereby record the approximate location of each COTS, iii) depth, iv) the proportion of the starfish that was visible from directly above as a measure of exposure, which will inform likelihood of detecting the same starfish using alternative survey methods, and v) whether the COTS was actively feeding, as well as taxonomic identity (mostly, genera) of all corals in the immediate vicinity that had feeding scars (conspicuous evidence of recent tissue loss over a relatively large and continuous portion of the colony).

In instances where COTS could not be found within the immediate vicinity of recent and conspicuous feeding scars (and were presumably hidden within the reef matrix or had moved away after feeding), the number of distinct sets of feeding scars (whereby multiple feeding scars within the same general vicinity were considered to be caused by a single COTS) were then added to the number of COTS sighted to infer overall COTS densities, following Chandler et al. (2023). We also calculated detectability at the level of each SALAD survey based on the ratio of number of COTS sighted (recorded density) to the inferred density.

Table 1. Number of SALAD surveys used to assess the distribution and abundance of COTS across four distinct regions between 2019 and 2024.

Region - Reef	2019	2020	2021	2022	2023	2024	Total
Cape Grenville			**18**	**24**	**28**	**12**	**82**
- McSweeney			6	6	12	4	28
- Monsoon				6	10	4	20
- U/N 11-049			6	6	6	4	22
- U/N 11-062			6				6
- U/N 11-060				4			4
- U/N 11-064				2			2
Princess Charlotte Bay			**24**	**18**	**22**		**64**
- Corbett			6	6	4		16
- U/N 13-124			6	6	8		20
- Davies			6				6
- U/N 13-040			6				6
- U/N 13-093				6	10		16
Lizard Island	**54**	**48**	**30**	**48**	**64**	**22**	**266**
- Lizard Island	36	38	22	36	25	10	167
- Eagle (Eyrie)	10	2	2	6	14	6	40
- North Direction	4	4	4	6	6		24
- MacGillIvray	4	4	2				10
- Martin					19	6	25
Cairns		**64**	**18**	**22**	**18**	**18**	**140**

Region - Reef	2019	2020	2021	2022	2023	2024	Total
- Thetford		22	6	8	6	6	48
- Moore		14	6	8	6	6	40
- Elford		22	6	6	6	6	46
- Milln		6					6
Total	**54**	**112**	**90**	**112**	**132**	**52**	**552**

The number and areal extent of SALAD surveys varied among reefs and regions (**Table 1**). The initial target was to complete at least six surveys at each of three different reefs within each region, though sampling was sometimes constrained by weather and/or opportunity. Likewise, there was disproportionate sampling undertaken at some reefs (especially, Lizard Island) where there was significant opportunity and need. More specifically, SALAD surveys were used whenever and wherever there was a need to ascertain the local densities and/or locate COTS for additional experiments (see Section 5).

2.2 Coral cover and habitat assessments

Spatiotemporal variation in coral cover and benthic composition was assessed using 50-m point intercept transects (PITs), both to assess how habitat condition influences abundance and detectability of COTS and test for localised effects of COTS, based on shifts in coral cover and/or composition. Two replicate point intercept transects were surveyed within the area encompassed by each SALAD survey, generally at the start and end of each survey, recording the specific organisms or type of substrate underlying each of 100 uniformly spaced points (50 cm apart) along each transect, following Pratchett et al. (2009). Corals were mostly identified to genus (using contemporary, molecular-based classifications for scleractinian corals). We also distinguished major growth forms for *Acropora* spp. (tabular, staghorn, and other) and *Porites* spp. (massive versus branching). Macroalgae were identified to genus. For survey points that did not intersect corals or macroalgae, the underlying substratum was categorised as either sponge, sand/rubble or carbonate pavement. Further, the proportional cover of crustose coralline algae (CCA) versus turf algae across relevant carbonate substrates (pavement and rubble) was recorded for each transect.

Topographic complexity was visually estimated at the start of each transect, using the six-point scale formalised by Wilson et al. (2007), which ranges from 0, where there is no vertical relief (essentially flat homogenous habitat) to 5, where there is very high topographic complexity, both at small scales (cm; provided by complex corals) and at larger scales (m), with numerous caves and overhangs. Topographic complexity is expected to vary spatially, partly in accordance with variation in coral cover.

2.3 Environmental DNA (eDNA) sampling for adult COTS

Environmental DNA (eDNA) refers to indirect genetic signatures of a species occurrence or abundance, which may be measured based on the natural occurrence of “free” DNA within water samples (e.g. Uthicke et al. 2018). The utility of eDNA for detecting COTS was demonstrated by Uthicke et al. (2018), whereby COTS were consistently detected in water samples taken from reefs in the central GBR during active population irruptions. Rather than detecting when and where population irruptions occur, eDNA sampling is likely to have greatest utility in detecting the local presence or occurrence of COTS on reefs with very limited densities (Doyle and Uthicke 2021; Uthicke et al. 2024b), thereby complementing SALAD surveys in the early detection of new or renewed population irruptions.

To test for concordance between eDNA Sampling and SALAD surveys, complementary sampling has been undertaken at a total of 82 sites, across 21 reefs and in multiple regions of the GBR, as far back as 2019 (**Table 2**). Importantly, sampling has been undertaken across locations with vastly different estimates of COTS densities, ranging from 0 to > 60 COTS.ha^{-1}. To test for the local occurrence and abundance of adult COTS using eDNA, 12 replicate 2,500 ml water samples were taken at each site by directly filtering the prescribed volume of water through a filter membrane that were measured for the presence of COTS eDNA. Successive samples were taken from the same location with virtually continuous water sampling (only stopping to allow sufficient time to change water filters and flush the system) between samples. Specific details of sampling methods and control protocols for eDNA sampling are outlined in the final report for CCIP-D-03 (Uthicke et al. 2025; see also Pratchett et al. 2022).

Table 2. Sampling sites used to compare independent estimates of local COTS abundance using eDNA Sampling and SALAD surveys.

Region - Reef	2019	2020	2021	2022	2023	Total
Cape Grenville			**9**	**12**	**3**	**24**
- McSweeney			3	3	1	7
- Monsoon				3		3
- U/N 11-049			3	3	2	8
- U/N 11-062			3			3
- U/N 11-060				2		2
- U/N 11-064				1		1
Princess Charlotte Bay				**6**	**2**	**8**
- U/N 13-124				3	2	5
- U/N 13-093				3		3
Lizard Island	**4**	**4**	**4**	**6**	**6**	**24**
- Lizard Island	4	4	4	4	4	20
- North Direction				2	2	4
Cairns		**4**		**2**	**2**	**8**
- Thetford		2		2	2	6
- Elford		2				2
Townsville		**3**			**15**	**18**
- Rib		2				2

Region - Reef	2019	2020	2021	2022	2023	Total
- Kelso		1				1
- Lynchs					4	4
- Darley					3	3
- Banfield					2	2
- Davies					2	2
- Prawn					2	2
- Faith					1	1
- Shrimp					1	1
Total	**4**	**11**	**13**	**26**	**28**	**82**

2.4 Data analyses

The primary purpose of this study was to test for interannual changes in the abundance of COTS across each of the four distinct regions: Cape Grenville, Princess Charlotte Bay, Lizard Island, and Cairns. Analyses of abundance considered combined counts of all COTS recorded as well as additional distinct sets of feeding scars where COTS were not detected. All analyses were conducted using Generalised Linear Mixed Models (GLMM) with the MASS Package (Ripley et al. 2013) in R, comparing across the four years of sampling (2021, 2022, 2023, and 2024), including data collected in 2021 as part of the CCIP early-investment project (Pratchett et al. 2022). Total counts were analysed using negative binomial distributions (with log link functions), which provided much better fit relative to comparable models using a Poisson distribution. Increasingly complex models were considered to assess whether variation in abundance of COTS could be explained based on year of sampling, proportional coral cover, and/or zone. All models included reef as a random factor and treated the area sampled as an offset. Alternative models were compared using corrected Akaike information criterion (AICc), with analysis of deviance shown for only the best model (**Appendix A: Table 3**).

Detectability of COTS was analysed using GLMMs with a binomial distribution (with a logit link function), given our ratio ranged from 0 to 1 and the range of values were highly constrained at low COTS densities (i.e. where there was only one set of feeding scars, the detectability could only be 0 or 1). The simplest model considered overall differences in detectability among regions. Increasingly complex models considered whether coral cover varied with local densities of COTS (inferred densities), habitat complexity, coral cover, zone and/or year of sampling. It was expected that detectability may increase with increasing emergence of adult COTS through time, thereby contributing to apparent increases in densities (*sensu* Houk and Raubani 2010), though our estimates of abundance also accounted for apparent feeding scars. Alternative models were compared using AICc, with analysis of deviance presented for only the best model (**Appendix A: Table 4**).

The proportional exposure of COTS that were sighted was also analysed to test for spatiotemporal variation in exposure. As for detectability, analyses were conducted using a binomial distribution (with a logit link function), as a very large proportion of COTS were either completely concealed (exposure = 0; 43.7%) or completely exposed (exposure = 1; 27.8%). The simplest model considered variation in exposure among regions. Increasingly complex models considered whether exposure varied with year and/or size of individual starfish. Alternative models were compared using AICc, with analysis of deviance presented for only the best model (**Appendix A: Table 5**).

Spatiotemporal variation in proportional coral cover was analysed using GLMMs with a quasibinomial distribution, to account for variation inherent within proportional cover estimates. However, to compare among alternative models it was necessary to use a binomial distribution (with a logit link function). The simplest model considered overall differences in coral cover among regions. Increasingly complex models considered whether coral cover varied with time (among years), and/or in accordance with local densities of COTS (inferred densities). It was expected that coral cover would decline among years in regions with highest densities of COTS, whereas coral cover may increase among years in regions where there were low densities of COTS (*sensu* Pratchett 2010). Alternative models were compared using AICc (based on binomial distributions), with analysis of deviance presented for only the best model and using a quasibinomial distribution (**Appendix A: Table 6**).

To compare independent estimates of COTS abundance, we directly compared the proportion of positive detections (from eDNA sampling) to inferred densities (accounting for both COTS sighted and feeding scars on SALAD surveys) using a Generalised Linear Model (GLM). Given vagaries in water flow and residence times, data were aggregated to test for variation among (rather than within) individual reefs, relating reef-wide estimates of the abundance of COTS based on the overall proportion of filters at the level of the reef (where number of replicates is the number of sites multiplied by 12) with positive detections of COTS (above prescribed limits of detection) with the average density of COTS recorded across relevant SALAD surveys. Site level contrasts are presented in Lawrence et al. (2025).

2.5 Stakeholder engagement

The objectives and outputs of this project were underpinned by considerable engagement with various stakeholders, particularly managers of the COTS Control Program at the Great Barrier Reef Marine Park Authority (the Reef Authority). The data from this project was regularly shared with managers from the Reef Authority and discussed at COTS control prioritisation meetings. Our team was also joined by Dr Rick Abom from the Reef and Rainforest Research Centre (RRRC), who compiled a short-documentary-style information video, which was later edited, shared with CCIP, and published on the RRRC LinkedIn webpage. This video explains the background and methods of this project (CCIP-P-04) and can be viewed by all stakeholders, including reef managers, COTS Control staff and Traditional Owners.

The project team contacted Traditional Owner (TO) groups in the regions where field sampling was planned, including Wuthathi Aboriginal Corporation (Cape Grenville), Yintjingga Aboriginal Corporation (Princess Charlotte Bay), Hope Vale Congress Aboriginal Corporation RNTBC (Lizard Island), Yirriganydji TUMRA Group (Cairns), and Girringun Aboriginal Corporation (Townsville), to communicate information about the project and begin building relationships. In one instance, Wuthathi Aboriginal Corporation, consent for the proposed research was explicitly withheld, and it was not possible to resolve this within the required timeframe of the proposed research, and so surveys were restricted to areas outside of the relevant Sea Country. Regular contact was made with all TO groups to update them on project progress and alert them to annual research plans. Given the logistical and funding constraints it was not possible to have TO representatives accompany us on annual research voyages, but this will be key to future engagement and needs to be included in project planning and budgets from the outset.

Project updates and data were shared and discussed with stakeholders, particularly reef managers, on an ongoing basis. This included presentations on this project (CCIP-P-04) at CCIP symposia and the Reef Resilience Symposium in 2024, and workshop-style or informal discussions with reef managers (and other stakeholders) to share information and/or receive feedback and maximise project and program pathway to impact. This significant two-way engagement, particularly with reef managers, throughout the duration of this project ensured that project objectives and outputs were well aligned with what is required to improve the ecological underpinning of COTS population modelling and management.

3. RESULTS

3.1 Density of crown-of-thorns starfish

A total of 552 SALAD surveys were conducted across 20 reefs, within the four study regions, from 2019 until 2024 (**Table 1**), with a combined survey area of 2,775,438 m^2, or 277.54 hectares. The total area sampled during each distinct SALAD survey averaged 4,933.05 m^2 (±10.61 SE), and varied depending on habitat structure, as well as local abundance and detectability of COTS. A total of 1,161 COTS, as well as a further 1,142 distinct sets of feeding scars, were recorded across all SALAD surveys, resulting in an average inferred density (including sets of scars) of 11.64 COTS.ha^{-1} (±0.67 SE). Mean densities recorded were substantially higher in the Cape Grenville region (17.45 COTS.ha^{-1} ±1.47 SE) and the Lizard Island region (14.01 COTS.ha^{-1} ±1.17 SE), compared to the Princess Charlotte Bay region (8.52 COTS.ha^{-1} ±1.53 SE) and the Cairns region (5.15 COTS.ha^{-1} ±0.50 SE).

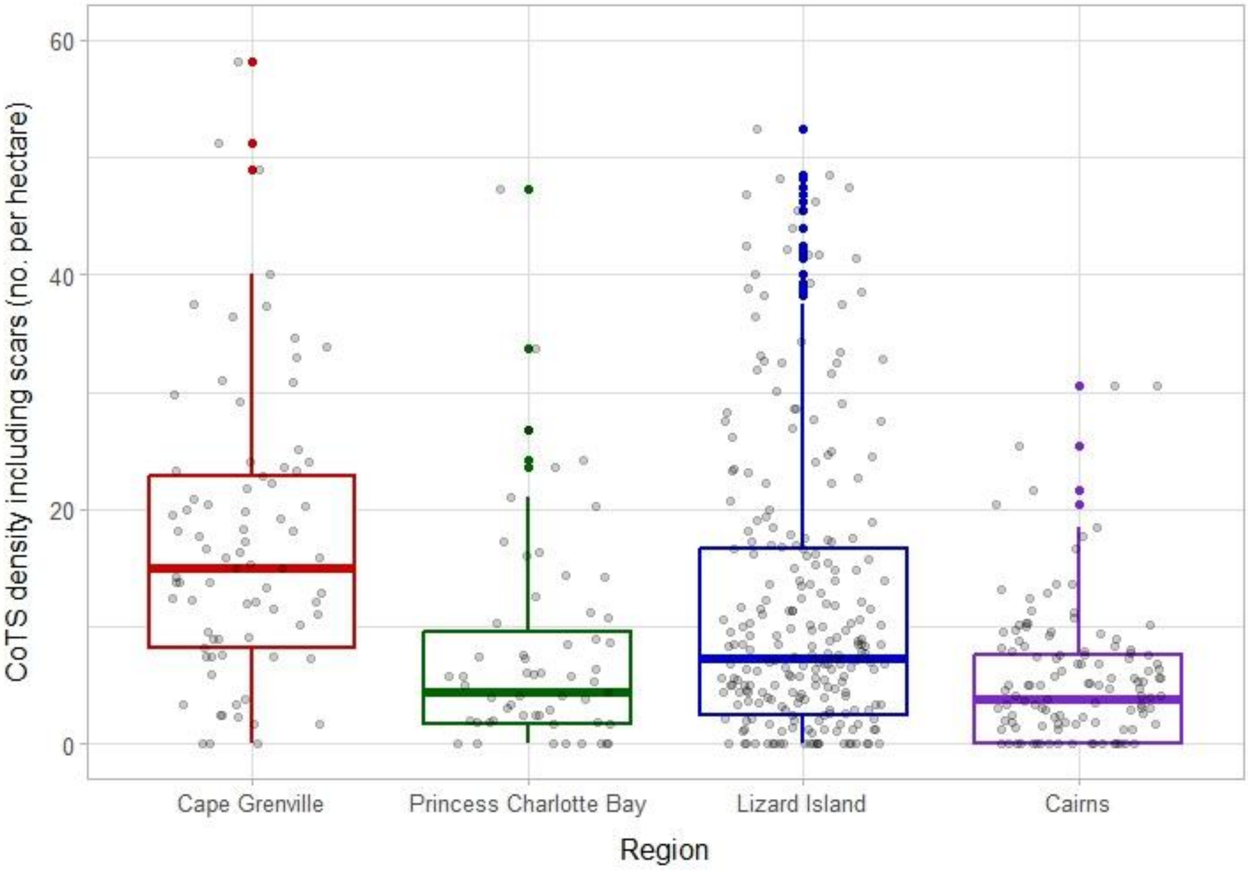

Figure 5. Box plots showing regional variation in COTS densities within each of 4 distinct regions (ordered north to south, see **Figure 3**) from 2021-2024. Each data point represents a SALAD survey. All data is presented as number of COTS recorded as well as the number of distinct sets of feeding scars where COTS were undetected, and standardised for differences in areal extent of different surveys (no. per hectare).

The best model to account for spatiotemporal variation in inferred COTS densities (taking account of distinct sets of feeding scars as well as COTS recorded) included an interaction between region and year of survey, while also accounting for local cover of hard corals (**Appendix A: Table 3**). The interaction between region and year is reflected in differential patterns of interannual variation among regions, whereby inferred densities increased from 2021 to 2024 in the Lizard Island region, but were relatively stable in the Cape Grenville and Princess Charlotte Bay regions (noting no surveys were conducted in the Princess Charlotte Bay region in 2024) and declined in the Cairns region (**Figure 6**; see also **Figure 7**). Recorded densities of COTS increased with increasing coral cover (**Figure 7**), suggesting that areas with high coral cover were supporting increased densities of COTS, and that high densities of COTS were yet to cause localised coral depletion.

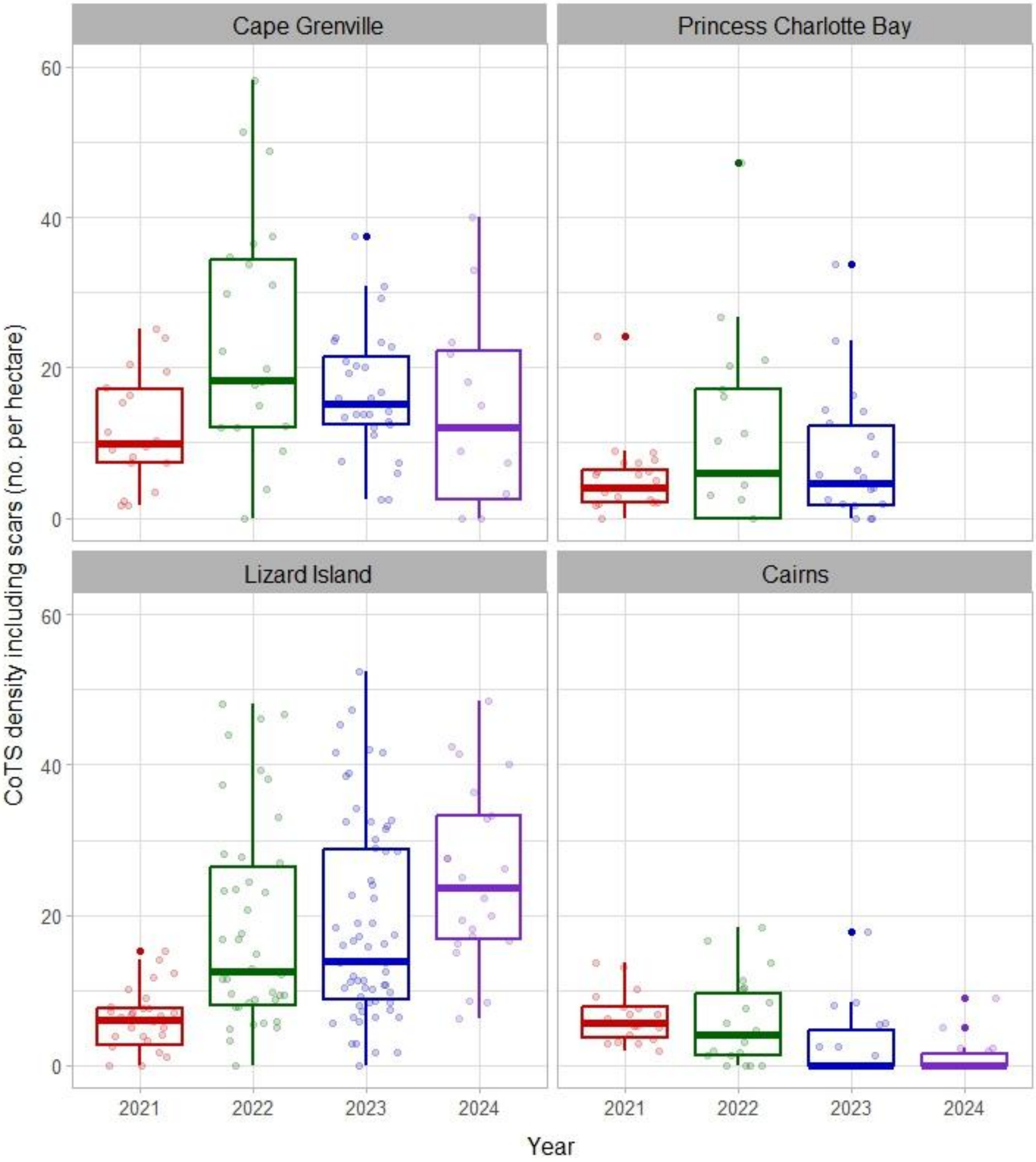

Figure 6. Box plots showing annual variation in COTS densities within each of four distinct regions. Each data point represents a SALAD survey. All data is presented as number of COTS recorded as well as the number of distinct sets of feeding scars where COTS were undetected, and standardised for differences in areal extent of different surveys (no. per hectare).

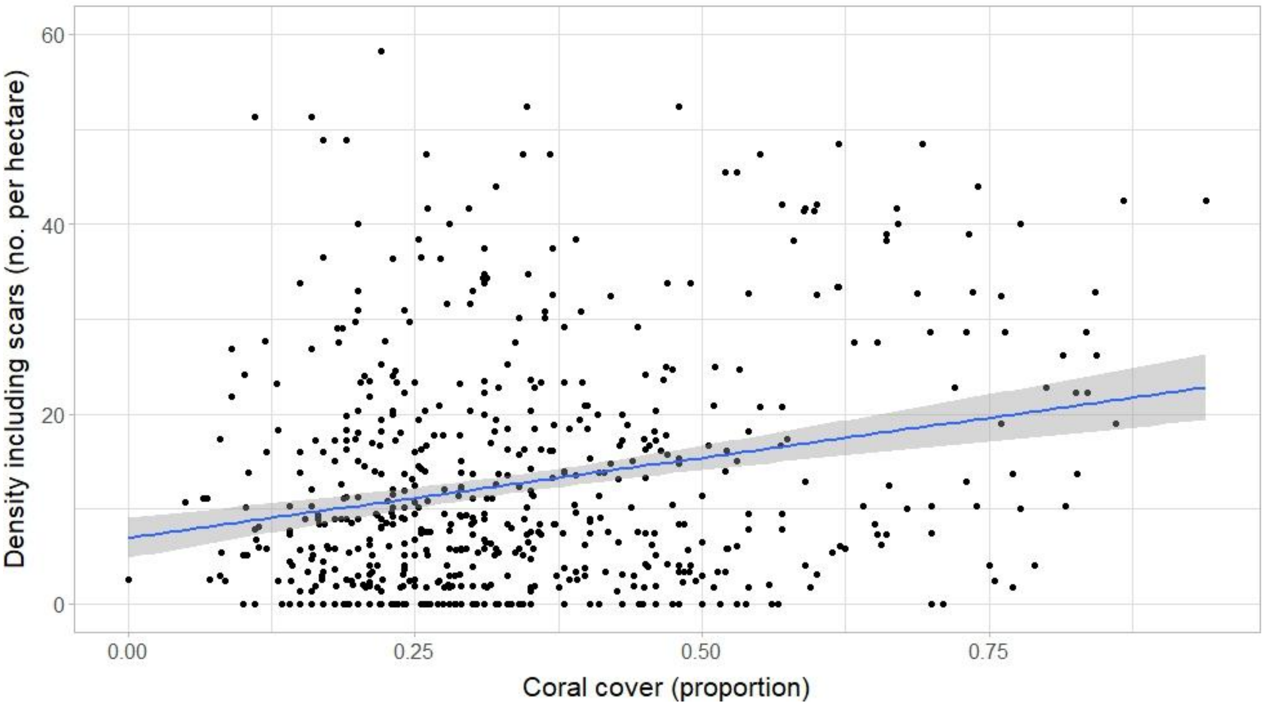

Figure 7. Relationship between inferred density of COTS (including scars) and proportional cover of hard corals, across all regions and years. Each data point represents a SALAD survey, whereby coral cover was estimated using 50 m point intercept transects at the start and end of each SALAD survey.

3.2 Detectability and exposure of crown-of-thorns starfish

Overall detectability of COTS (based on the ratio of recorded densities to inferred densities, where the latter included feeding scars) was estimated to be 47.25% across all SALAD surveys where COTS or feeding scars were recorded (n = 518 surveys). Detectability varied greatly among surveys ranging from 0–100% in every region (**Figure 8**). Detectability was highest in the Cape Grenville region (averaging 59.46% ±2.96 SE) and Lizard Island region (49.85% ±2.30 SE) where COTS were generally larger (see Section 3.3). Detectability was comparatively much lower in the Princess Charlotte Bay region (41.01% ±4.91 SE) and Cairns region (36.85% ±3.21 SE) (**Figure 8**).

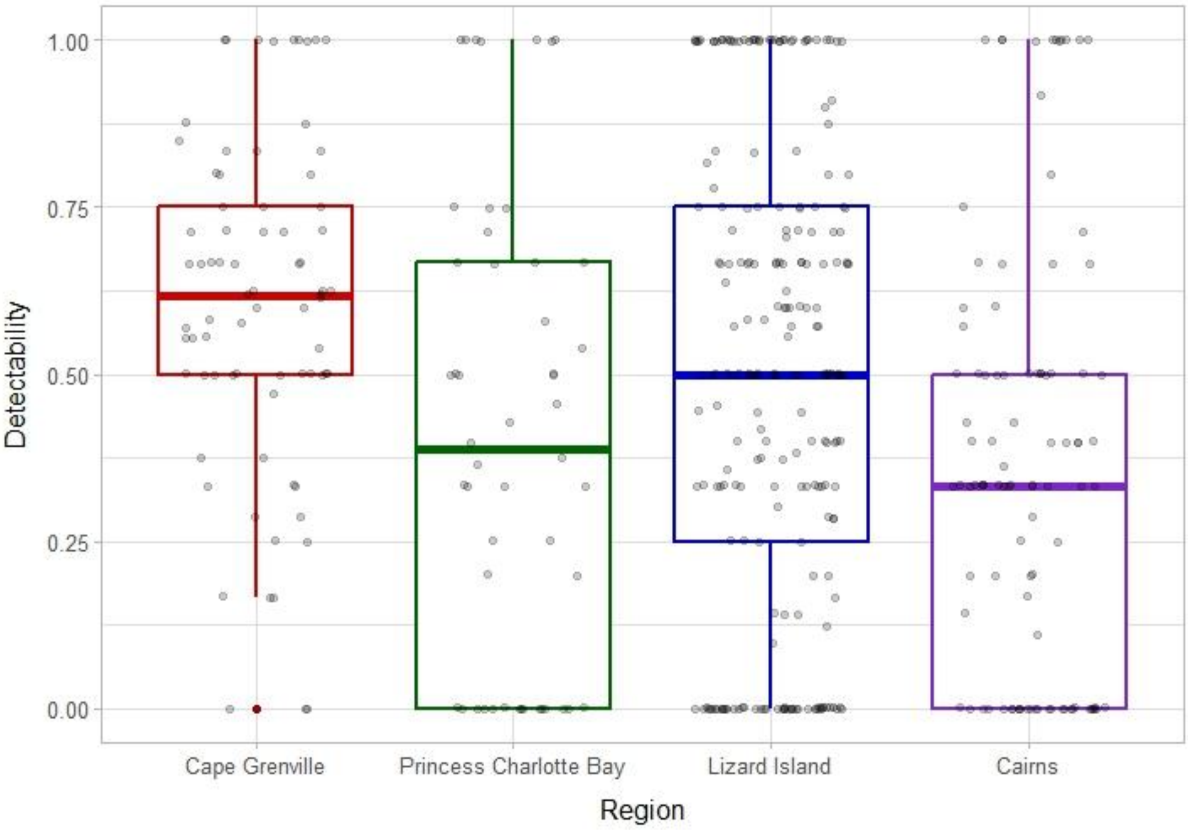

Figure 8. Box plots showing detectability of COTS densities within each of the four distinct regions. Each data point represents a SALAD survey. Detectability is calculated based on the ratio of COTS recorded (recorded densities), to overall inferred density, where the latter included the number of distinct sets of feeding scars where COTS were undetected.

The best model to account for spatiotemporal variation in detectability of COTS included only region and coral (**Appendix A: Table 4**), showing that there was limited additional information provided when considering year of sampling, nor the local density of COTS. The detectability recorded in the Cairns region was significantly lower than for Cape Grenville and Lizard Island regions, but not different from that recorded in the Princess Charlotte Bay region.

For starfish that were detected, the proportion of the starfish that was visible from directly above (exposure) was generally ≤ 0.5 (65.2%, n = 1,170), and a large proportion of starfish (43.7%, n = 1,170) were completely concealed from above and generally hidden well within the reef matrix. Conversely, 27.8% of starfish were completely exposed. The majority of starfish that were completely exposed (exposure = 1.0) were recorded in the Cape Grenville region, where 73.5% of starfish recorded were completely exposed. The mean level of exposure was substantially higher at Cape Grenville (0.83 ±0.02 SE), than at Princess Charlotte Bay (0.30 ±0.04 SE), Lizard Island (0.35 ±0.01 SE), and Cairns (0.14 ±0.02 SE) (**Figure 9**).

The best model to account for spatiotemporal variation in exposure of COTS included region as well as size of individual starfish (**Appendix A: Table 5**), showing that there was limited change in exposure among years. Exposure varied significantly among regions, which was likely explained by differences in the size structure of COTS (see Section 3.3). Notably, COTS < 250 mm diameter were most likely to be completely concealed, but exposure increased with size from 250 mm diameter to 500 mm (**Figure 10**).

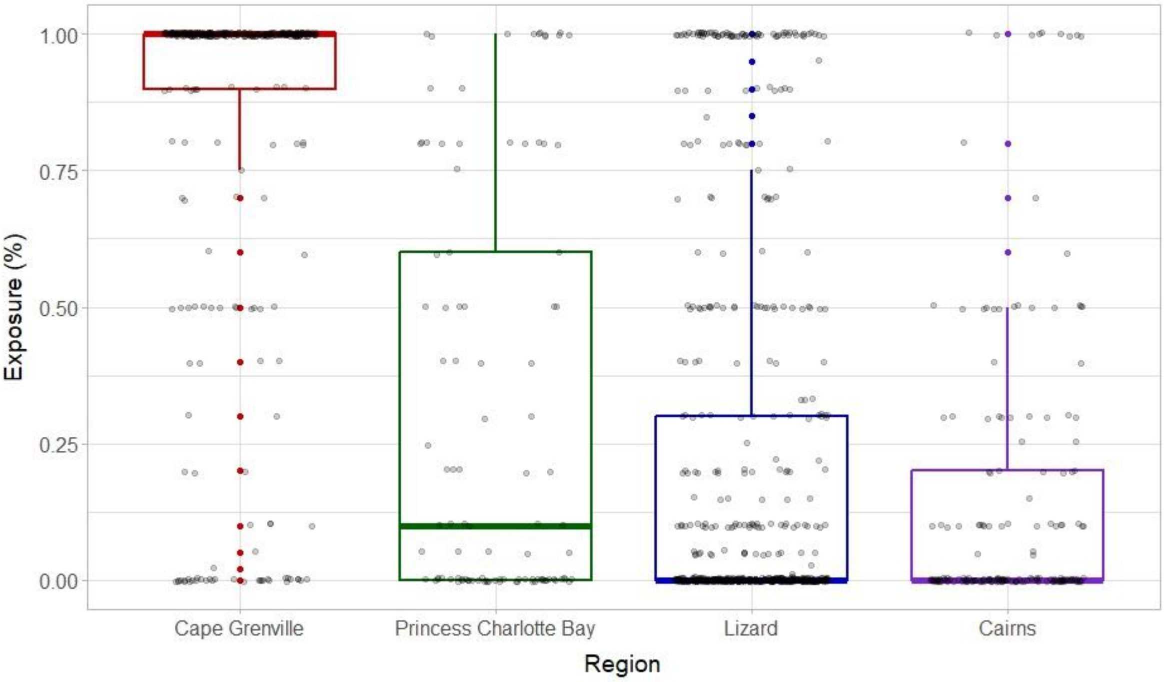

Figure 9. Box plots showing exposure of COTS densities within each of four distinct regions. Each data point represents an individual starfish that was sighted during SALAD surveys. Exposure is the proportion of the starfish that is visible from directly above.

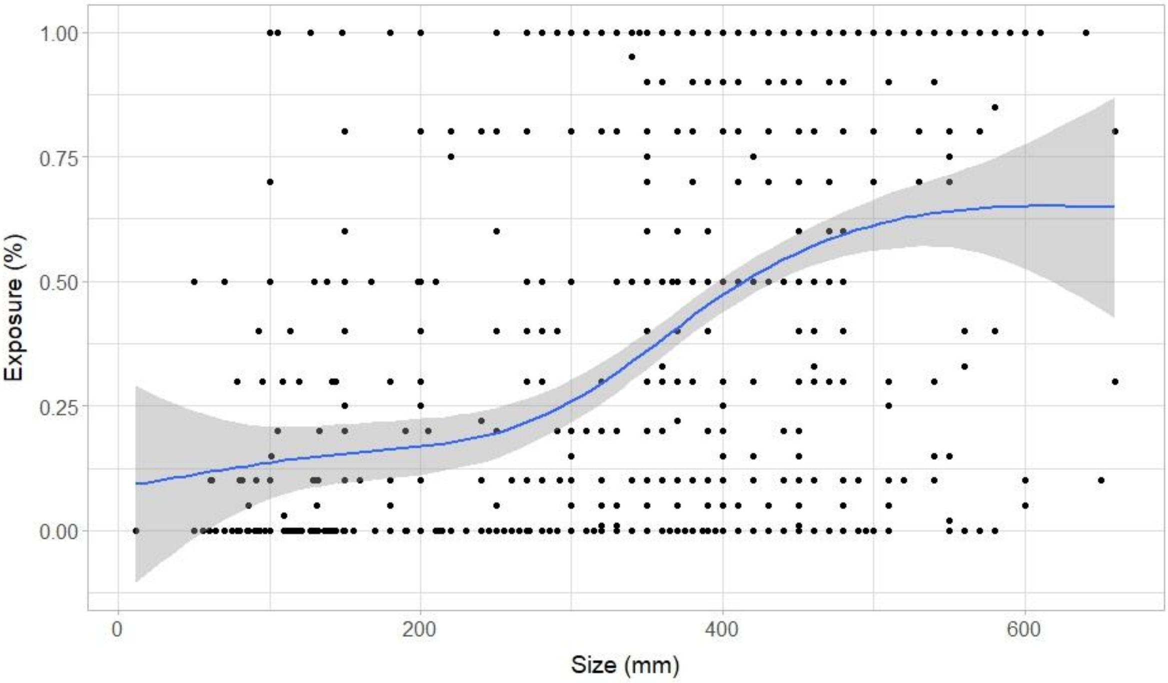

Figure 10. Relationship between exposure and size (diameter, in mm) of COTS, across all regions and years. Each data point represents an individual starfish that was sighted during SALAD surveys. Exposure is the proportion of the starfish that is visible from directly above.

3.3 Size structure of crown-of-thorns starfish

The size (diameter) of COTS recorded during SALAD surveys in the northern and far northern GBR (n = 969), from 2021–2024, ranged from 12 to 660 mm diameter, though the majority (85%) of COTS were between 250 and 530 mm diameter (**Figure 11**). Larger COTS (> 500 mm diameter) were recorded exclusively in the Cape Grenville and Lizard Island regions. The mean diameter of COTS recorded varied markedly among regions; Cape Grenville region (404.8 mm ±4.05 SE, n = 325); Princess Charlotte Bay region (247.5 mm ±9.53 SE, n = 101); Lizard Island region (392.5 mm ±4.18 SE n = 496); Cairns region (289.8 mm ±13.20 SE, n= 47). Within the Lizard Island region, mean size of COTS consistently increased among survey years: 2021 (348.9 mm ±12.45 SE, n = 62), 2022 (356.15 mm ±6.79 SE, n = 135), 2023 (413.23 mm ±6.06 SE, n = 229), 2024 (433.43 mm ±9.57 SE, n = 70). Elsewhere, and especially in the Cape Grenville region, there was limited interannual change in the size of COTS (**Figure 11**).

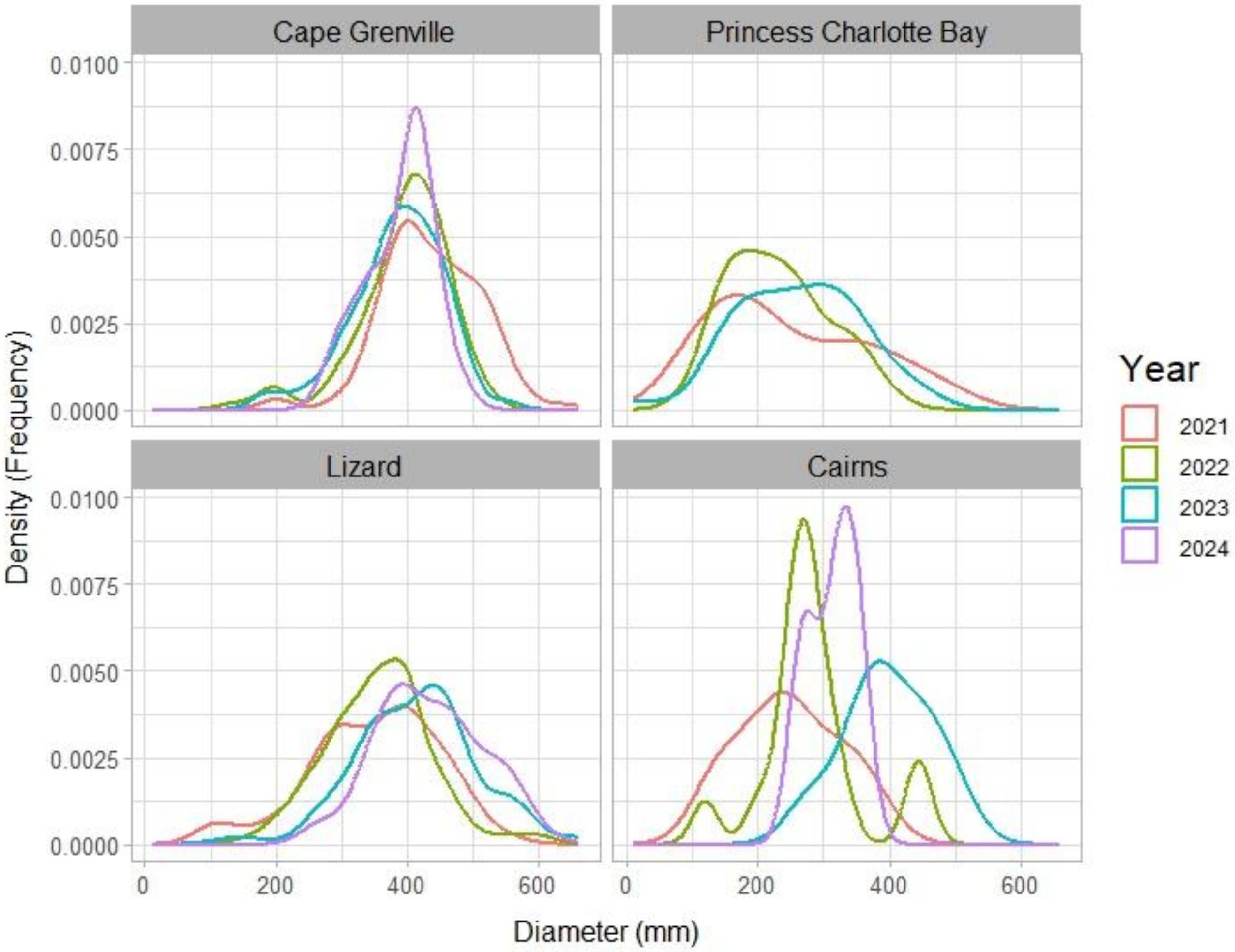

Figure 11. Size frequency distributions of COTS for each year (2021–2024) within each of the four distinct regions. The diameter of COTS recorded varies markedly among regions; Cape Grenville Region, mean = 404.8 mm (n =

325); Princess Charlotte Bay Region, mean = 247.5 mm (n = 101); Lizard Island Region, mean = 392.5 mm (n = 496); Cairns Region, mean = 289.8 mm (n= 47).

3.4 Changes in coral cover

Overall cover of hard coral recorded (order Scleractinia) during this study was 34.4% (±0.07 SE, n = 644), averaged across regions (Cape Grenville, Princess Charlotte Bay, Lizard Island and Cairns) and years (2021–2024). The highest coral cover was recorded at Lizard Island 44.8% (±0.14 SE), where coral cover increased appreciably from 39.36% (±0.41 SE) in 2021 to 52.95% (±0.32 SE) in 2024 (**Figure 12**). In other regions, coral cover was low and appeared to decline from 2021 to 2024. In the Cape Grenville region, for example, mean coral cover recorded in 2021 was 30.82% (±0.21 SE), but declined to 23.67% (±0.16 SE) by 2024. Temporal declines in coral cover in the Cape Grenville region may be attributable to the relatively larger size and higher density of COTS (see Sections 3.1 and 3.3), though overall variation in coral cover (within and among regions) cannot be readily explained by the local size or abundance of COTS. Notably, recorded coral cover was much lower in Cairns than at Lizard Island (**Figure 12**), and appeared to decline from 2023 to 2024, though there were very few COTS recorded in the Cairns region.

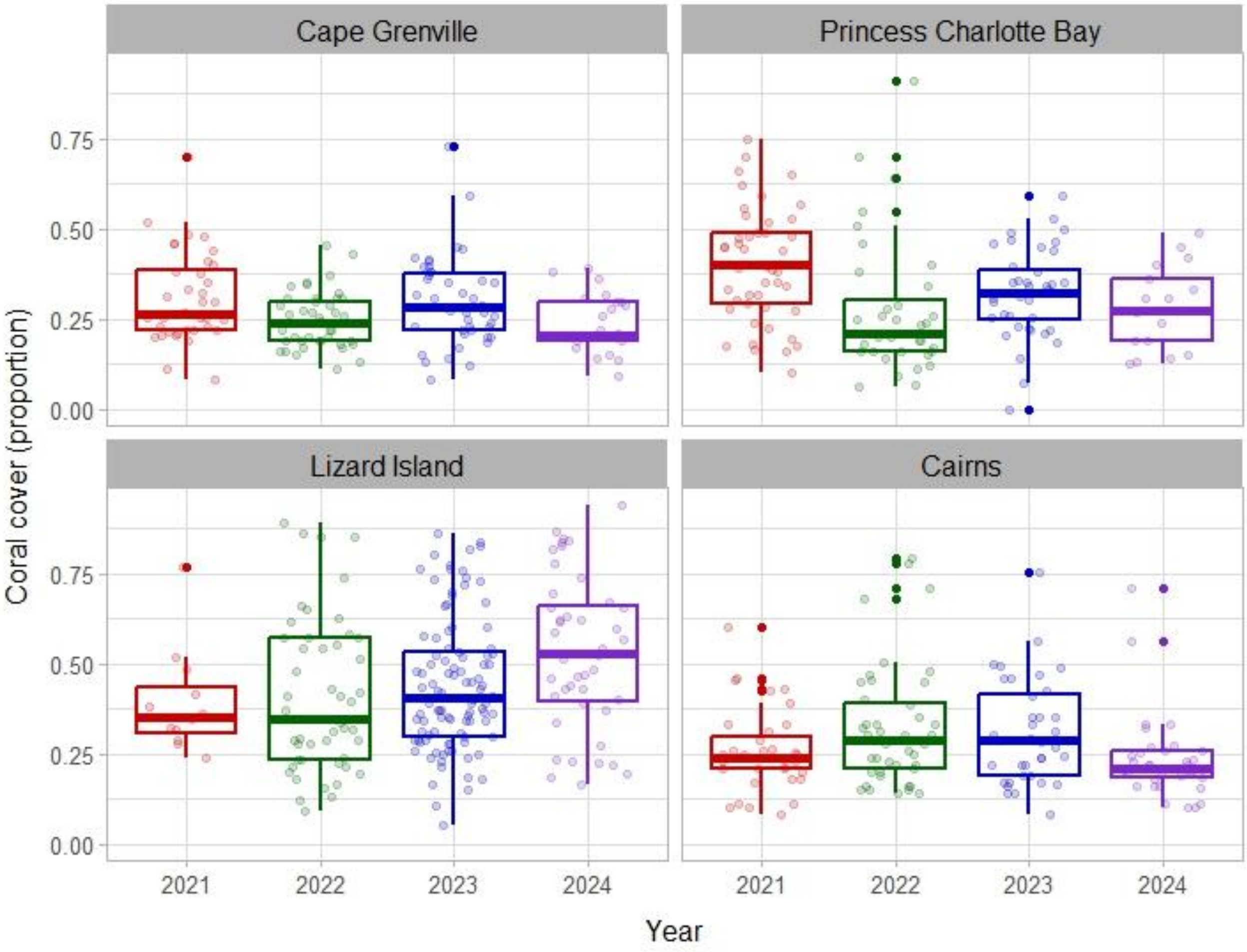

Figure 12. Box plots showing proportional cover of hard (order Scleractinia) corals in each year (2021–2024, within each of four distinct regions. Each data point represents data obtained using a 50-m point intercept transect. Coral

cover is calculated based on the overall proportion of all 100 sampling points that intercepted corals, regardless of the underlying habitat structure; transects were generally run in areas with negligible (if any) sand substrate.

The best model (noting all models had to be initially compared using the binomial, rather than quasibinomial) to explain spatiotemporal variation in coral cover included region and the density of COTS (**Appendix A: Table 6**), whereby year of sampling did not improve the model. It was apparent however, that coral cover increased over time in the Lizard Island region, whereas coral cover tended to decline in all other regions (**Figure 12**). However, the variation recorded among regions was much higher than variation recorded within regions, suggesting that local COTS population were yet to exert a major effect on local coral cover. Similarly, the relationship between COTS densities and coral cover was positive (**Figure 7**), suggesting that coral cover was influencing the abundance of COTS rather than *vice versa*.

3.5 Reef-level contrasts between eDNA and SALAD

Complementary sampling using diver-based (SALAD surveys) and diver-independent (eDNA) sampling methods to assess the local abundance of COTS was undertaken at 82 sites across 21 reefs (**Table 2**). To explore broadscale patterns and avoid any assumptions about the relevant scale necessary to ensure independent eDNA sampling, data was compared at the scale of reefs by year. While recorded densities are strongly and positively related to the inferred densities of COTS, the relationship between COTS density and proportion of eDNA samples that were positive of COTS, was compared for both recorded and inferred densities. A very high proportion of replicate water samples from sites sampled in the Cape Grenville regions had positive detections of eDNA for COTS (approaching 1.0), which is also where the highest densities of COTS were recorded (up to 40.32 COTS.ha^{-1}). Elsewhere, the proportion of eDNA samples in which COTS were detected was highly variable among reefs and years. In all, the proportion of water samples (averaged across replicate samples taken at all sites) in which COTS were detected ranged from 0.03 (at Davie Reef in Princess Charlotte Bay, which was sampled in 2021), up to 1.00 (e.g. McSweeney Reef in the Cape Grenville region). The recorded density of COTS across these same reefs and years, ranged from 0.0 COTS.ha^{-1} (whereby no COTS were recorded at Elford Reef in 2023) up to 24.90 COTS.ha^{-1} (at Cape Grenville in 2022). There was also a strong (adjusted r^2 = 0. 52) and significant positive relationship (lm log(Recorded_Density) ~ eDNA, p<0.001) between recorded density (log transformed) and proportion of eDNA samples positive for COTS (**Figure 13**). Similarly, there was a significant positive relationship (lm log(Inferred_Density) ~ eDNA, p<0.001) between inferred density (log transformed) and proportion of eDNA samples positive for COTS (**Figure 13**), though the relationship was not quite as strong (adjusted r^2 = 0.41).

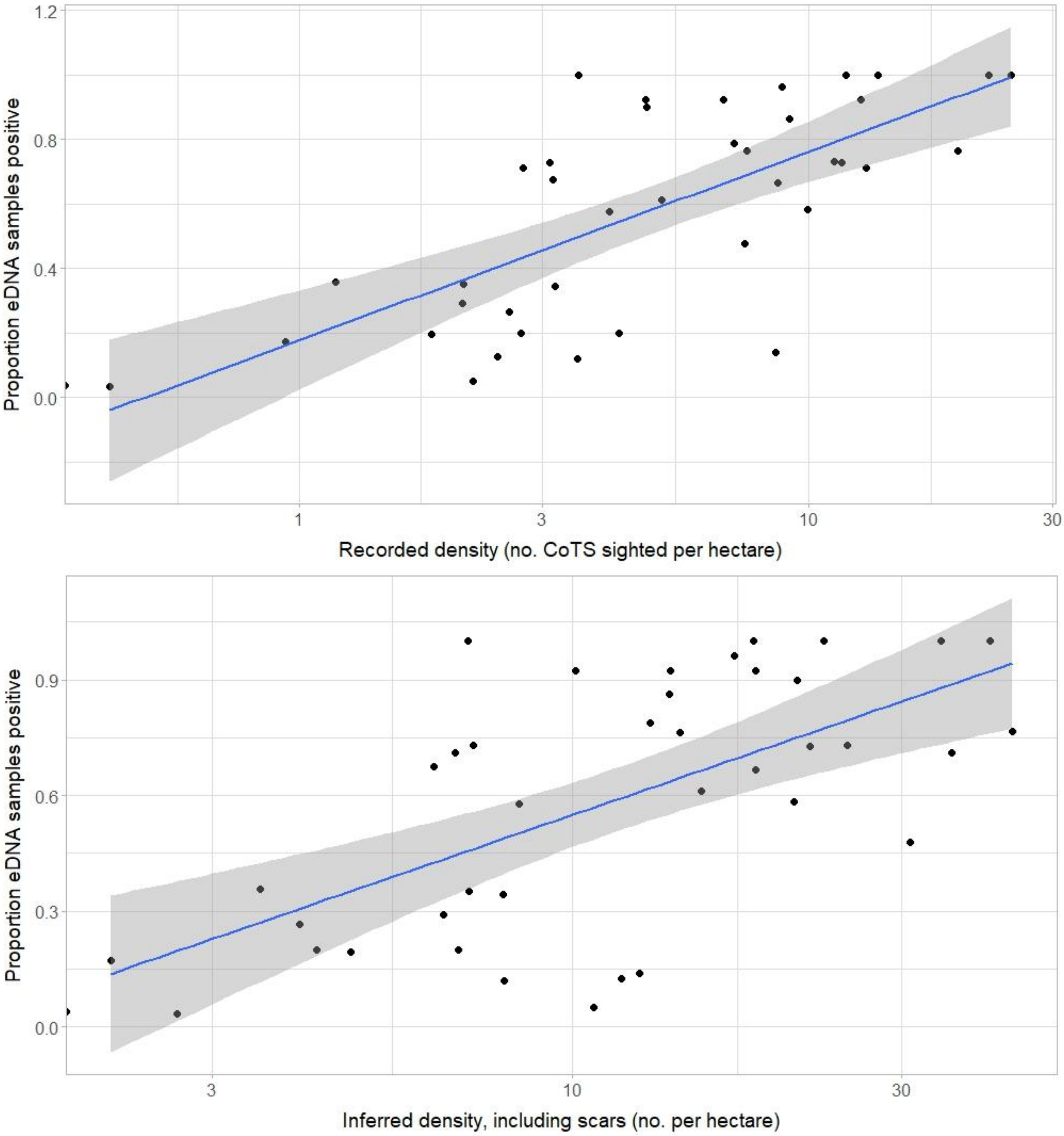

Figure 13. Relationship between recorded density (top panel) and inferred density (bottom panel) of COTS (determined using in-water SALAD surveys) with proportion of water samples taken at matched sites that were positive for COTS eDNA. Each data point represents a given reef sampled in a given year.

4. DISCUSSION AND OUTPUTS

This study revealed elevated densities of COTS at several reefs in the northern and far northern GBR, suggesting that renewed population irruptions have now commenced (see also Chandler et al. 2023; Uthicke et al. 2024b). More specifically, recurrent SALAD surveys since 2019 have resolved sustained increases in inferred densities of COTS at Lizard Island (**Figure 14**, which have now exceeded the notional threshold density (> 15 COTS.ha^{-1}; De'ath and Moran 1998) for population irruptions on the GBR. Renewed population irruptions were expected to occur on the GBR in 2025–2027 based on the periodicity (15–17 years) of previous population irruptions (Babcock et al. 2020). However, the purported timing of the initiation of previous population irruptions was based on the detection of already elevated densities (Sweatman et al. 1998; Pratchett 2005; see Section 1.3), and there was limited capacity to effectively survey COTS populations and detect initial increases in COTS densities. Accordingly, broadscale surveillance in the Lizard Island region, which has been ongoing, has reported limited detection of COTS and no outbreaks up until 2023–2024 (AIMS 2024). Given the unprecedented capacity to survey COTS and resolve subtle changes in abundance using SALAD surveys, it is not surprising that renewed population irruptions have been detected earlier than expected (Chandler et al. 2023).

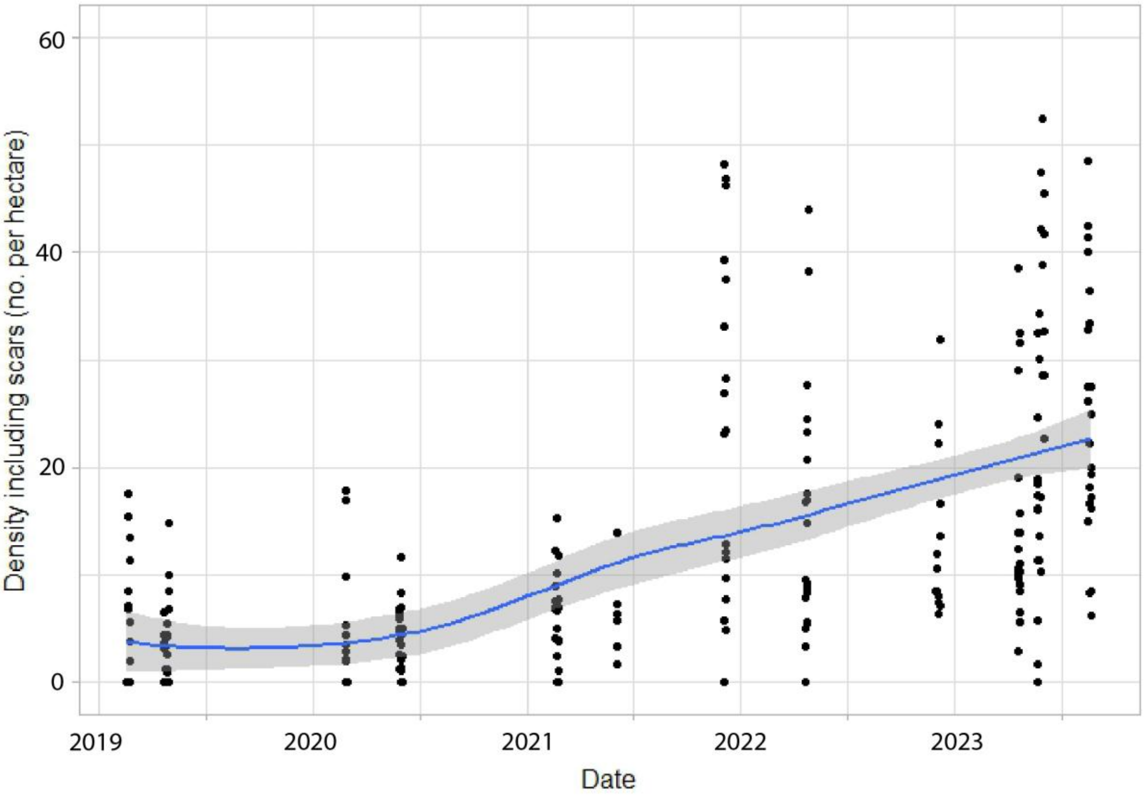

Figure 14. Temporal trends in inferred densities of COTS at Lizard Island, based on SALAD surveys (n = 616) conducted from August 2019 until February 2024. Inferred densities were fairly stable (at ~2.5 COTS.ha^{-1}) up until mid-2020, after which there were sustained increases. Surveys were conducted at least twice per calendar year at Lizard Island, except in 2024.

Recurrent sampling at Lizard Island since August 2019, using SALAD surveys, revealed limited change in mean densities from 2019–2020; while inferred densities of COTS were highly variable among SALAD surveys conducted in 2019 and 2020 (ranging from 0 to >15 COTS.ha^{-1}), the mean density was relatively stable during this period, at 2.27 COTS.ha^{-1} (±0.29 SE). This may represent the normal, background (non-outbreak) density of COTS at this location, which is congruent with the modelled Allee threshold of < 3 COTS.ha^{-1} (Rogers et al. 2017). This may explain the apparent stability of COTS populations at Lizard Island from 2019–2020, though it is unclear what caused the subsequent increases (from 2021). This is considered a critical knowledge gap for understanding and modelling population dynamics, and especially factors that lead to population irruptions (McCallum 1987; Reichelt et al. 1990). From 2020–2021, there were sustained increases in inferred densities across successive surveys (conducted at least twice per year) up until February 2024 (**Figure 14**). This shows that increases in COTS densities may occur several years before population irruptions are clearly apparent at individual reefs, and initiation of population irruptions is caused by protracted increases in COTS densities, at least at this location (see also Pratchett 2005). While these data still do not resolve the underlying causes of population irruptions, which may be attributable to a combination of natural phenomena and anthropogenic pressures (Babcock et al. 2016a), protracted increases in the COTS densities do at least present opportunities to constrain population growth, and thereby contain (if not prevent) renewed population irruptions.

Population irruptions of COTS on the GBR, and throughout the Indo West-Pacific, are generally recorded based on the seemingly sudden appearance of elevated COTS (Moran 1986; Pratchett et al. 2024), whereas there have been very few studies that have documented protracted increases in COTS densities in the lead up to population irruptions (Zann et al. 1990; Sweatman et al. 1998; Pratchett 2005). It is often assumed, therefore, that population irruptions of COTS arise due to abrupt changes in population size (e.g. Houk and Raubani 2010), though changes in apparent densities may be partly attributable to density-dependent changes in the behaviour and exposure of COTS (Moran 1986). Notably, COTS are purported to be much more cryptic (and largely nocturnal) at low densities (Chesher 1969), whereas increasing densities (and corresponding competition for coral prey) may lead to a seemingly rapid emergence of relatively large COTS once they transition to feeding throughout the day (Moran 1986). Accounting for changes in detectability of COTS is therefore critical in understanding patterns and processes involved in the initiation of population irruptions.

4.1 Detectability of COTS and consequences for monitoring

Detectability is the Achilles heel of effective monitoring and management for pest organisms (e.g. Hayes et al. 2005; Britton et al. 2011), though detectability of COTS has rarely been considered, let alone quantified (MacNeil et al. 2016). However, there is extensive anecdotal evidence that standard visual surveys conducted during daylight hours detect less than 50% of COTS present in a given area (e.g. Babcock et al. 1994). Current surveillance programs (e.g. manta tow and culling) are also highly sensitive to observer bias when estimating abundance. Emerging diver-independent methods (e.g. eDNA) will provide opportunities for validation and ground-truthing of detectability to help reduce or better standardise observer bias. In the meantime, the few studies that have quantified detectability of COTS, using mark re-capture (MacNeil et al. 2016), or comparing densities recorded during the day to those obtained in same location at night (Kayal et al. 2017) suggest that the detectability of COTS is generally high (73–82%). However, these studies considered only larger adults, and were also conducted using intensive small-scale (transect-based) surveys. Overall detectability recorded in this study (47.25%) was much lower than reported previously, which may be because it accounts for even the smallest size classes of coral feeding COTS. It is recognised that detectability will be much lower for smaller individuals and will vary depending on specific survey method (e.g. MacNeil et al. 2016). Detectability is also likely to vary depending on coral cover habitat structure, and corresponding changes in behavioural modality (Moran 1986). Indeed, regional differences in detectability reflected differences in the size of COTS, though it was not possible to explicitly assess whether detectability varied with the size of COTS (i.e. not possible to know the size of starfish that were not sighted). Estimates of detectability presented herein, also do not account for the imperfect detection of feeding scars, which will further underestimate the density of COTS.

Given limited detectability and recognised constraints in assessing local abundance of COTS (e.g. MacNeil et al. 2016), evidence of recent feeding activity (conspicuous feeding scars) is often used as a proxy for COTS presence and abundance (e.g. Plass-Johnson et al. 2015; Kayal et al. 2017). Accounting for feeding scars may improve accuracy of abundance estimates for COTS, though there are limitations and potential biases to this approach. Most critically, it is challenging to discern COTS feeding scars from other causes of coral mortality (e.g. feeding activities of *Drupella* spp. and other corallivorous invertebrates) without carefully inspecting individual coral colonies. It is also very difficult to distinguish distinct sets of feeding scars (attributable to each individual starfish), especially if COTS densities are very high, or coral mortality caused by COTS is compounded by other disturbances (e.g. severe coral bleaching). It is likely therefore, that the inferred densities reported in this study represent underestimates, not only because we do not account for detection of feeding scars, but because it was necessarily assumed that distinct clusters of feeding scars were caused by a single COTS. Moreover, not all COTS will necessarily leave conspicuous evidence of recent feeding activity. These biases are expected to scale with COTS density, and in particular, reduced separation among adjacent starfish, wherein it will be increasingly challenging to distinguish distinct sets of feeding scars attributable to individual starfish. Accounting for feeding scars will, therefore, have greatest utility for resolving low densities of COTS, which are important for understanding and managing the initiation of population irruptions.

4.2 The initiation of population irruptions on the GBR

While difficult to rigorously categorise or quantify (Potts 1981; Pratchett et al. 2014), population irruptions of COTS are characterised by conspicuous increases in local densities of adult starfish, and corresponding ecological impacts, especially relative to normal baseline or predominant population states (Moran and De'ath 1992; Hoey et al. 2016). Much of the confusion regarding the occurrence of population irruptions arises due to differences in the scale of population assessments and areas of interest, e.g. considering what happens at an individual reef (Pratchett 2005) versus broadscale consideration of interconnections across an entire reef system (Bozec et al. 2021). Critically, the patterns and processes involved in the primary initiation versus secondary spread of population irruptions are very different and have important management connotations (Pratchett et al. 2014). It has generally been accepted that the primary initiation of population irruptions was driven by protracted increases in local densities of COTS over several successive recruitment events, leading to gradual accumulation of starfish across multiple cohorts, reflected in a wide range of different size and age classes (Stump 1996; Pratchett 2005). The enhanced reproductive potential of established population irruptions then gives rise to subsequent (secondary) population irruptions on downstream reefs (Kenchington 1977). Sustained increases in the abundance of COTS recorded at Lizard Island (**Figure 14**; see also Sweatman et al. 1998; Pratchett 2005) might be considered typical of a primary initiation, though it is necessary to understand the predominant source of larvae that is giving rise to these population increases. The primary initiation of a population irruption is expected to result from the progressive accumulation of starfish in areas with high levels of self-recruitment (Moore 1990), whereby larvae settling in the Lizard Island region would largely represent the progeny of adult starfish from this region. Conversely, sustained increases in COTS populations may reflect continued input of larvae from upstream reefs, whereby it is the relatively low levels of larval supply that explain the gradual and protracted increases in COTS densities recorded at Lizard Island.

Identifying where recurrent episodes of population irruptions of COTS start is central to understanding and managing the putative cause(s) of these recurrent disturbances on the GBR (Pratchett et al. 2014; Babcock et al. 2016a; Westcott et al. 2020). Notably, direct interventions (e.g. culling or removing individual starfish) are inherently constrained in their scale (Pratchett and Cumming 2019), requiring concerted effort to effectively suppress COTS densities to levels that minimise or prevent localised coral loss (Westcott et al. 2020). Long-term or large-scale solutions, therefore, require explicit consideration of the underlying cause(s) of population irruptions, and/ or highly targeted direct interventions to prevent or contain new and emerging population irruptions (Babcock et al. 2020; Matthews et al. 2024).

Persistent uncertainties regarding the ultimate cause(s) of population irruptions relate, at least in part, to inherent constraints associated with effectively sampling and monitoring COTS populations outside of major population irruptions (Moore 1990; Pratchett et al. 2017). Moore (1990) suggested that there are likely to be distinct differences in the biology and behaviour of COTS populations during population irruptions compared to persistent low-density populations. Most notably, Moore (1990) suggested that persistent low-density COTS populations must be inherently constrained by extrinsic processes, such as limited prey availability, that constrain individual condition and population dynamics. There may also be important regional differences in environmental and habitat conditions that facilitate differences in baseline densities (Moore 1990), which may be critical for understanding where population irruptions initiate. However, limited studies on the biology and behaviour of COTS outside of major population irruptions make it difficult to test these hypotheses. In this study, the initial and seemingly stable densities of COTS recorded in the Cape Grenville region (17.45 COTS.ha^{-1} ±1.47 SE), were substantially higher than that recorded in the Princess Charlotte Bay region (8.52 COTS.ha^{-1} ±1.53 SE), though it is unknown whether these data reflect stable or persistent baseline densities of COTS at reefs sampled in each of these regions.

The increased abundance of COTS recorded at Cape Grenville in 2021 (relative to other regions) was originally considered to represent the early initiation of a population irruption, which was expected to proliferate in subsequent years (Pratchett et al. 2022). Conversely, it may be that COTS densities had already peaked in this region, and that subsequent sampling would reveal local population crashes coinciding with localised depletion of prey corals. However, there was relatively limited change in recorded densities of COTS in the Cape Grenville region during subsequent sampling (**Figure 6**), and also limited evidence of corresponding coral depletion (**Figure 12**). Moreover, the size structure of COTS populations in the Cape Grenville region were remarkably stable (**Figure 11**). It is possible, therefore, that COTS densities recorded in the Cape Grenville region (17.45 $COTS.ha^{-1}$ ±1.47 SE) represent normal (non-outbreaking) baseline densities, though there is limited long-term data to test this hypothesis. If so, this would suggest that reefs in the Cape Grenville region support higher baseline densities of COTS compared to other regions considered, which, rather than being a precursor of reef-wide population irruptions, may be an important contributor to the origination of population irruptions at other downstream reefs (see Moore 1990). Critically, ongoing annual sampling (using current or complementary methods) is needed to understand the status and relevance of seemingly elevated COTS densities at reefs in the Cape Grenville region.

4.3 Putative causes of renewed population irruptions

The capacity of COTS to undergo population irruptions is fundamentally linked to their life-history (Uthicke et al. 2009), and especially their exceptional reproductive capacity (Babcock et al. 2016b; Pratchett et al. 2021b). However, the initiation of population irruptions is generally ascribed to extrinsic factors that moderate underlying population dynamics, whether it be acute increases in reproductive success due to relaxation of normal predatory constraints on adult size (e.g. Endean 1969) or spawning behaviour (Cowan et al. 2017), or increased nutrients in coastal waters that enhance larval survival and development (Birkeland 1982; Brodie et al. 2005). On the GBR, recurrent population irruptions have been variously ascribed to major flood events (Fabricius et al. 2010) and/or apparent differences in dynamics of COTS populations and incidence of population irruptions on reefs where fishing is or is not permitted (Sweatman 2008), which is ascribed to differences in predation pressure imposed upon COTS by target reef fish species (McCallum 1987; Kroon et al. 2021). However, the seemingly consistent periodicity of recurrent population irruptions (see Babcock et al. 2020) is probably best explained by coupled oscillations in abundance of COTS and their coral prey (e.g. Bradbury et al. 1985).

The data presented herein may necessitate a re-thinking of the idea that initiation of reef-wide population irruptions of COTS on the GBR occurs within the initiation area (**Figure 3**), in either the Lizard Island region (Pratchett 2005) and/or the Cairns region (Wooldridge and Brodie 2015). While recurrent surveys (since 2019) present evidence of increasing COTS densities at Lizard Island (**Figure 14**), suggesting that renewed population irruptions have commenced, elevated densities of COTS were already apparent in the Far Northern GBR (Cape Grenville region), well before the densities at Lizard Island approached notional outbreak thresholds (**Figure 6**). More research is needed to establish whether the elevated densities of COTS recorded in the Cape Grenville region represent the initiation of a population irruption, as well as ascertaining links between these elevated densities and corresponding increases in COTS densities recorded at Lizard Island (see Section 5). However, midshelf reefs in the Cape Grenville region are far removed from anthropogenic and coastal processes, making it difficult to ascribe the potential initiation of population irruptions in this area to either fishing or nutrient inputs. More likely is that elevated densities of COTS on reefs sampled in the Cape Grenville region are attributable to high levels of self-recruitment that have allowed for the progressive accumulation of starfish in recent years, while local constraints on population size (due to either predatory regulation or limited suitable coral prey) have prevented severe population irruptions from occurring (see Moore 1990). If so, the only relevant and effective management action will be to undertake concerted culling within this region. Improving water quality and further restricting fisheries will, however, have benefits for reef heath and resilience regardless of whether they reduce or prevent the future incidence of population irruptions of COTS on the GBR (Pratchett et al. 2014).

While extrinsic drivers of apparent increases in COTS densities recorded in the Cape Grenville and Lizard Island regions are equivocal, this study provides unprecedented opportunities to test for changes in the biology and behaviour of COTS during the apparent initiation of renewed population irruptions. As discussed previously, there is very limited data on fine-scale changes in the population structure and dynamics of COTS in the period immediately preceding an outbreak (Moran 1986), which makes it difficult to establish the ultimate or proximal cause(s) of population irruptions (Moore 1990). Notably, there was no apparent temporal change in the detectability of exposure of COTS occurring alongside recorded increases in the abundance of COTS. Rather, detectability and exposure were consistently high in the Cape Grenville region and less so, in the Lizard Island region (**Figure 8** and **Figure 9**), which is mainly attributable to the larger size of COTS occurring on these reefs. This would suggest that emergence of COTS (*sensu* Houk and Raubini 2010) has a limited role in explaining recorded increases in COTS densities, but may be important in areas where population irruptions arise from mass recruitment of a single cohort of COTS. Changes in the detectability and exposure of COTS are also likely to have significant effects on densities of COTS reported using rapid and large-scale survey methods (e.g. manta tows).

4.4 Key outputs of this project

The key outputs of this project are:

- Development and application of SALAD surveys, a novel and effective method to provide highly resolved estimates of COTS densities, especially at low to moderate COTS densities. This method complements existing survey approaches for establishing large-scale patterns in incidence of population irruptions (e.g. manta tows) and is particularly important for assessing and understanding the initiation of new and renewed population irruptions.

- New knowledge on spatiotemporal variation in the abundance and population structure of COTS across four years (2021–2024) and four distinct regions in the Northern (Cairns and Lizard Island regions) and Far Northern (Princess Charlotte Bay and Cape Grenville regions) sectors of the GBR. Most critically, this study has highlighted the potential importance of elevated COTS densities in the Far Northern GBR, which may represent or facilitate renewed population irruptions on the GBR.

- Unprecedented data on the abundance and population structure of COTS, as well as coral cover and habitat structure, from a range of reefs both inside and outside of the putative *initiation area*, based on sampling that commenced in 2019 (albeit at a subset of reefs) and has been undertaken annually up to and including 2024. These data complement information obtained from other large-scale (AIMS LTMP) or intensive surveillance programs (e.g. periodically undertaken by the field management program) but are particularly useful in providing highly resolved estimates of COTS abundance using complementary sampling to test for inter-annual changes in the size and structure of COTS populations.

- Extensive eDNA data from the Northern and Far Northern GBR, which reinforces findings from in water SALAD surveys, and further contributes to the demonstrated utility of both these methods for detecting low densities of COTS and the early initiation of population irruptions.

5. RESEARCH SYNERGIES AND NEXT STEPS

The research conducted in this project (CCIP-P-04) compliments other CCIP projects both within and beyond the Prediction Subprogram (**Figure 2**). Most notably, this research project has been conducted in conjunction with several other projects within the Prediction Subprogram (especially, CCIP-P-01 Pratchett et al. 2025 and CCIP-P-06 Doll et al. 2025), which collectively contribute to improved understanding of the ecological context in which population irruptions of COTS occur, recognising that COTS not only have a major influence on the structure and function of coral reef ecosystems, but are in turn, strongly influenced by changing environmental and habitat conditions across the GBR (e.g. Caballes et al. 2016). Ultimately, this research will enable much more accurate predictions regarding spatiotemporal variation in the abundance and dynamics of COTS populations, which will facilitate more efficient and effective operational responses.

Fundamentally, this project presents a novel survey method (SALAD surveys) that complements existing monitoring and surveillance tools (e.g. manta tow), greatly increasing opportunities for improved detection and monitoring, which contributes directly to the broader outcomes and impacts of CCIP (**Figure 2**). The utility of SALAD surveys was assessed alongside complementary survey methods in CCIP-D-02 (Lawrence et al. 2025), highlighting the specific capacity to provide highly resolved estimates of local abundance, especially at low to moderate COTS densities. This has primary importance in understanding the patterns and processes involved in the initiation of population irruptions, providing unprecedented insights into the underlying changes in dynamics of COTS populations and increasing opportunities for targeted management. Importantly, the best opportunity to mitigate effects of COTS at the scale of the entire GBR, using current techniques and available resources, may be to undertake pre-emptive culling in key initiation areas to prevent or contain renewed population irruptions (Babcock et al. 2020; Matthews et al. 2024). Complementary sampling using both SALAD surveys and eDNA sampling was also facilitated through the course of this project, making maximum use of expeditions to the Far Northern sector of the GBR.

Aside from facilitating pre-emptive culling to suppress apparent increases in COTS densities and thereby prevent (or contain) new or renewed population irruptions, early detection and effective monitoring of population irruptions are critical for resolving persistent controversies regarding the cause(s) of population irruptions (Babcock et al. 2020; Chandler et al. 2023). Documenting coincidental or successive increases in COTS densities across a range of widely separated reefs will not, however, necessarily resolve the fundamental mechanisms leading to population irruptions. Most critically, it is important to assess the extent of high-density COTS populations across a much broader range of reefs in the Far Northern GBR, and also further explore potential linkages between established populations of large COTS in the Cape Grenville region and apparent increases in COTS densities at Lizard Island. Critically, potential hydrodynamic linkages need to verified with demonstrated ecological connectivity among reefs and regions in the northern and far northern sectors of the GBR. Preliminary hydrodynamic models (e.g. Hock et al. 2014) have highlighted the potential importance of reefs in the far northern GBR as a source of COTS larvae, while there is also evidence of potential southward flow in the far northern GBR especially during the summer months (Luik et al. 2007; Choukroun et al. 2025), though there has been extremely limited research in this region, especially compared to the area between Lizard Island and Cairns (see also CCIP-R-05 Choukroun et al.

2025). This project has contributed to necessary research in this area, with deployments of Marotte HS tilt current meters (in both 2022–2023 and 2023–2024) to validate and improve hydrodynamic models for the far northern GBR (CCIP-R-05 Choukroun et al. 2025), following Wolanski and Lambrechts (2020).

To understand potential drivers of the initiation of population irruptions of COTS on the GBR it is important to simultaneously assess spatiotemporal patterns in the abundance of COTS and corresponding variation in environmental and habitat conditions (Babcock et al. 2020). Of particular importance, is understanding larval connectivity, and spatiotemporal variation in larval retention, which may contribute to the initiation of population irruptions (Wooldridge and Brodie 2015).

5.1 Priorities for future research

The major priorities for future research and development that have emerged through this project, include:

- Ongoing sampling to resolve longer-term changes (or stability) in the population structure and abundance of COTS across the Far Northern GBR, using SALAD surveys or other complementary methods that can resolve low to moderate COTS densities. This is important to understand the role of seemingly elevated densities of COTS at reefs in the Cape Grenville region as precursors or contributors to emergence of renewed reef-wide population irruptions on the GBR.

- Genetic analyses of larval connectivity to verify the predominant source(s) of COTS settling at Lizard Island (and other locations throughout the northern GBR), thereby establishing whether sustained increases in population sizes reflect high levels of self-recruitment or continued low rates of larval supply from upstream reefs in the Far Northern GBR. This will require development of new and improved genetic markers and methods, as previous attempts using 26 polymorphic microsatellite markers (Harrison et al. 2015) have failed to provide sufficient resolution of population structure (Harrison et al. 2017). This may also be partly addressed by explicitly testing for stock-recruitment relationships across a range of different reefs and regions, which in itself is considered a critical knowledge gap and research priority (McCallum 1992; Pratchett et al. 2021a).

- Improved understanding of both larval dispersal and retention to better understand spatiotemporal variation in population dynamics, and especially population replenishment of COTS across different regions of the GBR. This will be partly aided through development of new and improved genetic markers to better resolve genetic structure of COTS populations, but also improved understanding of larval biology to inform fine-scale models of larval dispersal (see also CCIP-R-05 final report; Choukroun et al. 2025).

6. MANAGEMENT IMPLICATIONS AND IMPACT

Population irruptions of COTS remain one of the foremost causes of coral loss and reef degradation on the GBR (Mellin et al. 2019), and effective and recurrent monitoring of COTS populations is critical to inform ongoing management, both for improving understanding and prediction of the timing and location of population irruptions, as well increasing the efficiency and effectiveness of operational responses. This study has demonstrated the utility of two novel sampling methods, both SALAD surveys and eDNA sampling, which greatly increase the capacity to resolve spatiotemporal variation in the abundance of COTS and detect the early onset of population irruptions. These methods do not supersede or replace existing surveillance approaches (e.g. reef-wide manta tows), rather they are complementary methods that have specific utility for assessing and understanding population dynamics of COTS at low to moderate densities. Most critically, SALAD surveys and eDNA sampling have much greater capacity to resolve the early onset of renewed population irruptions (Chandler et al. 2023; Uthicke et al. 2024b), which is necessary for addressing many key knowledge gaps pertaining to the biology and ecology of COTS (e.g. Pratchett et al. 2017).

Improved understanding of patterns and processes involved in the primary initiation of population irruptions will have significant benefits for the long-term strategic management of COTS populations on the GBR, increasing opportunities to contain or prevent new and renewed population irruptions. SALAD surveys may further contribute to the COTS Control Program’s on-water operations and data collection, both to support and validate effectiveness of ongoing culling, especially in areas with low to moderate COTS densities. While there would be significant constraints to using SALAD surveys to document large-scale (e.g. across the geographical extent of the GBR) and long-term patterns in the incidence of population irruptions, its use provides unprecedented opportunities to resolve low densities of COTS, which should be used strategically to complement other broadscale monitoring methods.

If population irruptions of COTS are caused or exacerbated by anthropogenic activities, be it overfishing and/or eutrophication, redressing these issues would intuitively prevent or reduce the incidence of future population irruptions (Brodie et al. 2005). However, it is very challenging to effectively and rapidly reverse long-term and significant effects of anthropogenic activities in coastal environments (Fidelman et al. 2013; Hughes et al. 2017) and there is no certainty that these changes (if achieved) would necessarily affect the likelihood or incidence of future population irruptions (Pratchett et al. 2014). Direct management of population irruptions is therefore warranted, even if population irruptions of COTS are a natural phenomenon. Culling of individual starfish currently represents the most direct and effective method for regulating COTS populations (Westcott et al. 2020) and is one of the foremost management actions to reduce coral loss on the GBR and thereby enhance the resilience, structure, and function of reef ecosystems (Ortiz et al. 2018; Bellwood et al. 2019; Mellin et al. 2019; Bozec et al. 2021; Condie et al. 2021; Matthews et al. 2024). The efficiency and effectiveness of direct culling is however, conditional upon early detection and response (Matthews et al. 2024), further highlighting the utility and application of novel sampling methods (SALAD surveys and eDNA sampling) presented herein.

7. ACKNOWLEDGEMENTS

Sampling undertaken in the northern GBR (Cairns and Lizard Island regions from 2019–2020) was funded by the Ian Potter Foundation through the Australian Museum’s Lizard Island Research Station. In 2021, sampling in the Cairns and Lizard Island regions was funded by a Lizard Island Research Station Critical Research Grant, while complementary sampling in the far northern GBR (Princess Charlotte Bay and Cape Grenville) was funded by an Early-Investment grant from CCIP. All sampling from 2022–2024 was funded by CCIP (CCIP-P-04).

This research benefited greatly from field assistance provided by Andrew Baird, Deborah Burn, Genevieve Hennessy, Bethan Lang and Kai Pacey. The authors are also indebted to the owners, skippers and crew of charter vessels used to complete this research including Wild Blue, Aroona and Delphi.

All research presented in this report was approved by the Great Barrier Reef Marine Park Authority (Permit no. G21/45711.1).

8. DATA ACCESSIBILITY

All survey data has been stored in a single data repository and is accessible via eAtlas https://doi.org/10.26274/hjq7-tc71. The data has also been provided to the Great Barrier Reef Marine Park Authority and other relevant end-users.

9. REFERENCES

AIMS (2024) Coral cover remain high while impacts of mass coral bleaching yet to be determined. Annual summary report of the Great Barrier Reef condition 2023-2024. Australian Government, Australian Institute of Marine Science (AIMS) https://www.aims.gov.au/sites/AIMS_LTMP_Report__2023_2024_final.pdf

Babcock RC, Mundy CN, Whitehead D (1994) Sperm diffusion models and *in situ* confirmation of long-distance fertilization in the free-spawning asteroid *Acanthaster planci*. The Biological Bulletin 186(1):17-28. https://doi.org/10.2307/1542033

Babcock RC, Dambacher JM, Morello EB, Plagányi ÉE, Hayes KR, Sweatman HP, Pratchett MS (2016a) Assessing different causes of crown-of-thorns starfish outbreaks and appropriate responses for management on the Great Barrier Reef. PLoS ONE 11: e0169048. https://doi.org/10.1371/journal.pone.0169048

Babcock RC, Milton DA, Pratchett MS (2016b) Relationships between size and reproductive output in the crown-of-thorns starfish. Marine Biology 163: 1-7. https://doi.org/10.1007/s00227-016-3009-5

Babcock RC, Plagányi ÉE, Condie SA, Westcott DA, Fletcher CS, Bonin MC, Cameron D (2020) Suppressing the next crown-of-thorns outbreak on the Great Barrier Reef. Coral Reefs 39(5): 1233-1244. https://doi.org/10.1007/s00338-020-01978-8

Barnes JH (1966) The crown-of-thorns starfish as a destroyer of coral. Australian Natural History 15: 257-261.

Bellwood DR, Pratchett MS, Morrison TH, Gurney GG, Hughes TP, Álvarez-Romero JG, Day JC, Grantham R, Grech A, Hoey AS, Jones GP (2019) Coral reef conservation in the Anthropocene: confronting spatial mismatches and prioritizing functions. Biological Conservation 236: 604-615. https://doi.org/10.1016/j.biocon.2019.05.056

Benson AA, Patton JS, Field CE (1975) Wax digestion in a crown-of-thorns starfish. Comparative Biochemistry and Physiology Part B: Comparative Biochemistry 52(2): 339-340. https://doi.org/10.1016/0305-0491(75)90075-9

Birkeland C (1989) The Faustian traits of the crown-of-thorns starfish. American Scientist 77(2): 154-163.

Birkeland C (1982) Terrestrial runoff as a cause of outbreaks of *Acanthaster planci* (Echinodermata: Asteroidea). Marine Biology 69:175-185. https://doi.org/10.1007/BF00396897

Bozec YM, Hock K, Mason RA, Baird ME, Castro-Sanguino C, Condie SA, Puotinen M, Thompson A, Mumby PJ (2021) Cumulative impacts across Australia’s Great Barrier Reef: A mechanistic evaluation. Ecological Monographs 92(1): e01494. https://doi.org/10.1002/ecm.1494

Bradbury RH, Hammond LS, Moran PJ, Reichelt RE (1985) Coral reef communities and the crown-of-thorns starfish: evidence for qualitatively stable cycles. Journal of Theoretical Biology 113(1):69-80. https://doi.org/10.1016/S0022-5193(85)80076-X

Britton JR, Pegg J, Gozlan RE (2011) Quantifying imperfect detection in an invasive pest fish and the implications for conservation management. Biological Conservation 144(9):2177-2181. https://doi.org/10.1016/j.biocon.2011.05.008

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. https://doi.org/10.1016/j.marpolbul.2004.10.03

Caballes CF, Pratchett MS, Kerr AM, Rivera-Posada JA (2016) The role of maternal nutrition on oocyte size and quality, with respect to early larval development in the coral-eating starfish, *Acanthaster planci*. PLoS One 11(6): e0158007. https://doi.org/10.1371/journal.pone.0158007

Caballes CF, Byrne M, Messmer V, Pratchett MS (2021) Temporal variability in gametogenesis and spawning patterns of crown-of-thorns starfish within the outbreak initiation zone in the northern Great Barrier Reef. Marine Biology 168(1): 13. https://doi.org/10.1007/s00227-020-03818-3

Chandler JF, Burn D, Caballes CF, Doll PC, Kwong SL, Lang BJ, Pacey KI, Pratchett M (2023) Increasing densities of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) at Lizard Island, northern Great Barrier Reef, resolved using a novel survey method. Scientific Reports 13: 19306. https://doi.org/10.1038/s41598-023-46749-x

Chesher RH (1969) Destruction of Pacific corals by the sea star *Acanthaster planci*. Science 165(3890): 280-283. https://doi/abs/10.1126/science.165.3890.280

Choukroun S, Bode M, Stewart O, Porobic J, Langlais C, Lambrechts J, Mason L (2025) Crown-of-thorns starfish (COTS) connectivity modelling under multidimensional uncertainties on Australia’s Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program.

Condie SA, Anthony KR, Babcock RC, Baird ME, Beeden R, Fletcher CS, Gorton R, Harrison D, Hobday AJ, Plagányi ÉE, Westcott DA (2021) Large-scale interventions may delay decline of the Great Barrier Reef. Royal Society Open Science 8(4): 201296. https://doi.org/10.1098/rsos.201296

Cowan ZL, 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. https://doi.org/10.3390/d9010007

Cowan ZL, Ling SD, Caballes CF, Dworjanyn SA, Pratchett MS (2020) Crown-of-thorns starfish larvae are vulnerable to predation even in the presence of alternative prey. Coral Reefs 39: 293-303. https://doi.org/10.1007/s00338-019-01890-w

De'ath G, Moran PJ (1998) Factors affecting the behaviour of crown-of-thorns starfish (*Acanthaster planci* L.) on the Great Barrier Reef 1: Patterns of activity. Journal of Experimental Marine Biology and Ecology 220(1):83-106. https://doi.org/10.1016/S0022-0981(97)00085-3

Doll PC, Pratchett MS, Ling SD, Tebbett SB, Hoey AS, Caballes CF (2025) Predation on adult Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*, COTS) relative to fisheries management zones on Australia’s Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program.

Doyle J, Uthicke S (2021) Sensitive environmental DNA detection via lateral flow assay (dipstick)—A case study on corallivorous crown-of-thorns sea star (*Acanthaster* cf. *solaris*) detection. Environmental DNA 3(2): 323-342.

Endean RG (1969) Report on investigations made into aspects of the current *Acanthaster planci* (crown-of-thorns) infestations of certain reefs of the Great Barrier Reef. Queensland Department of Primary Industries (Fisheries Branch), Brisbane.

Endean R (1982) Crown-of-thorns starfish on the Great Barrier Reef. Endeavour 6(1): 10-14. https://doi.org/10.1016/0160-9327(82)90004-7

Endean R, Stablum W (1973) A study of some aspects of the crown-of-thorns starfish (*Acanthaster planci*) infestations of reefs of Australia's Great Barrier Reef. Atoll Research Bulletin. 167: 1-77.

Fabricius KE, 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. https://doi.org/10.1007/s00338-010-0628-z

Fernandes L, Marsh H, Moran PJ, Sinclair D (1990) Bias in manta tow surveys of *Acanthaster planci*. Coral Reefs 9(3): 155-160. https://doi.org/10.1007/BF00258228

Fidelman PI, Leitch AM, Nelson DR (2013) Unpacking multilevel adaptation to climate change in the Great Barrier Reef, Australia. Global Environmental Change 23(4): 800-812.

Foo SA, Millican HR, Byrne M (2024) Crown-of-thorns seastar (*Acanthaster* spp.) feeding ecology across species and regions. Science of The Total Environment 930: 172691. https://doi.org/10.1016/j.scitotenv.2024.172691

Goreau TF (1964) On the predation of coral by the spiny starfish *Acanthaster planci* (L.) in the southern Red Sea. Bulletin of the Sea Fisheries Research Station of Israel 35: 23-26.

Harrison HB, Saenz-Agudelo P, Al-Salamah M, Messmer V, Pratchett MS, Berumen ML (2015) Microsatellite multiplex assay for the coral-eating crown-of-thorns starfish, *Acanthaster* cf. *planci*. Conservation Genetics Resources 7: 627-630. https://doi.org/10.1007/s12686-015-0462-2

Harrison HB, Pratchett MS, Messmer V, Saenz-Agudelo P, Berumen ML (2017) Microsatellites reveal genetic homogeneity among outbreak populations of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on Australia's Great Barrier Reef. Diversity 9(1):16. https://doi.org/10.3390/d9010016

Hayes KR, Cannon R, Neil K, Inglis G (2005) Sensitivity and cost considerations for the detection and eradication of marine pests in ports. Marine Pollution Bulletin 50(8): 823-834. https://doi.org/10.1016/j.marpolbul.2005.02.032

Hock K, Wolff NH, Condie SA, Anthony KR, Mumby PJ (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. https://doi.org/10.1111/1365-2664.12320

Hoegh-Guldberg O (1999) Climate change, coral bleaching and the future of the world's coral reefs. Marine and Freshwater Research 50(8): 839-866. https://doi.org/10.1071/MF99078

Hoey J, Campbell M, Hewitt C, Gould B, Bird R (2016) *Acanthaster planci* invasions: applying biosecurity practices to manage a native boom and bust coral pest in Australia. Management of Biological Invasions 7(3): 213-220. https://doi.org/10.3391/mbi.2016.7.3.01

Houk P, Raubani J (2010) *Acanthaster planci* outbreaks in Vanuatu coincide with ocean productivity, furthering trends throughout the Pacific Ocean. Journal of Oceanography 66(3): 435-458. https://doi.org/10.1007/s10872-010-0038-4

Hughes TP, Baird AH, Bellwood DR, Card M, Connolly SR, Folke C, Grosberg R, Hoegh-Guldberg O, Jackson JB, Kleypas J, Lough JM (2003) Climate change, human impacts, and the resilience of coral reefs. Science 301(5635): 929-933. https://doi.org/10.1126/science.1085046

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC (2017) Global warming and recurrent mass bleaching of corals. Nature 543(7645):373-377.

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett MS, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science 359(6371): 80-83. https://doi.org/10.1126/science.aan8048

Kayal M, Vercelloni J, Lison de Loma T, Bosserelle P, Chancerelle Y, Geoffroy S, Stievenart C, Michonneau F, Penin L, Planes S, Adjeroud M (2012) Predator crown-of-thorns starfish (*Acanthaster planci*) outbreak, mass mortality of corals, and cascading effects on reef fish and benthic communities. PLoS One 7(10): e47363. https://doi.org/10.1371/journal.pone.0047363

Kayal M, Bosserelle P, Adjeroud M (2017) Bias associated with the detectability of the coral-eating pest crown-of-thorns seastar and implications for reef management. Royal Society Open Science 4(8):170396. https://doi.org/10.1098/rsos.170396

Keesing JK, Lucas JS (1992) Field measurement of feeding and movement rates of the crown-of-thorns starfish *Acanthaster planci* (L.). Journal of Experimental Marine Biology and Ecology 156(1) :89-104. https://doi.org/10.1016/0022-0981(92)90018-6

Kenchington RA (1977) Growth and recruitment of *Acanthaster planci* (L.) on the Great Barrier Reef. Biological Conservation 11(2):103-18. https://doi.org/10.1016/0006-3207(77)90032-5

Kenchington RA, Pearson R (1981) Crown of thorns starfish on the Great Barrier Reef: a situation report. Proceedings of the 4th International Coral Reef Symposium 2: 597-600.

Kenyon JC, Aeby GS (2009) Localized outbreak and feeding preferences of the crown-of-thorns seastar *Acanthaster planci* (Echinodermata, Asteroidea) on reefs off Oahu, Hawaii. Bulletin of Marine Science 84(2):199-209.

Kroon FJ, Barneche DR, Emslie MJ (2021) Fish predators control outbreaks of crown-of-thorns starfish. Nature Communications 12(1):6986. https://doi.org/10.1038/s41467-021-26786-8

Lawrence E, Foster S, Williamson D, Matthews S, Schultz D, Pratchett M, Uthicke S, Bainbridge S, Doyle J, Doll P, Armin A, Ewels C (2025) A comparison and calibration of crown-of-thorns starfish (COTS) and coral monitoring tools. A report to the Australian Government by the COTS Control Innovation Program.

Luick JL, Mason L, Hardy T, Furnas MJ (2007) Circulation in the Great Barrier Reef Lagoon using numerical tracers and in situ data. Continental Shelf Research 27(6):757-78. https://doi.org/10.1016/j.csr.2006.11.020

MacNeil MA, Mellin C, Pratchett MS, Hoey J, Anthony KR, Cheal AJ, Miller I, Sweatman H, Cowan ZL, Taylor S, Moon S (2016) Joint estimation of crown of thorns (*Acanthaster planci*) densities on the Great Barrier Reef. Peer J 4: e2310. https://doi.org/10.7717/peerj.2310

Matthews SA, Williamson DH, Beeden R, Emslie MJ, Abom RT, Beard D, Bonin M, Bray P, Campili AR, Ceccarelli DM, Fernandes L (2024) Protecting Great Barrier Reef resilience through effective management of crown-of-thorns starfish outbreaks. PLoS One 19(4): e0298073. https://doi.org/10.1371/journal.pone.0298073

McCallum HI (1987) Predator regulation of *Acanthaster planci*. Journal of Theoretical Biology. 127(2):207-220. https://doi.org/10.1016/S0022-5193(87)80131-5

McCallum HI (1992) Completing the circle: stock-recruitment relationships and *Acanthaster*. Marine and Freshwater Research 43(3): 653-662. https://doi.org/10.1071/MF9920653

Mellin C, Matthews S, Anthony KR, Brown SC, Caley MJ, Johns KA, Osborne K, Puotinen M, Thompson A, Wolff NH, Fordham DA (2019) Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global Change Biology 25(7): 2431-2445. https://doi.org/10.1111/gcb.14625

Moore RJ (1990) Persistent and transient populations of the crown-of-thorns starfish, *Acanthaster planci*. Lecture Notes in Biomathematics 88: 236-277.

Moran PJ (1986) The *Acanthaster* phenomenon. Oceanography and Marine Biology: An Annual Review 24: 379-480.

Moran PJ, De'Ath G (1992) Estimates of the abundance of the crown-of-thorns starfish *Acanthaster planci* in outbreaking and non-outbreaking populations on reefs within the Great Barrier Reef. Marine Biology 113: 509-515. https://doi.org/10.1007/BF00349178

Nash W, Zell LD (1981) *Acanthaster* on the Great Barrier Reef: distribution on five transects between 14 S and 18 S. Proceedings of the 4th International Coral Reef Symposium 2: 601-605.

Ormond RF, Campbell AC, Head SH, Moore RJ, Rainbow PR, Saunders AP (1973) Formation and breakdown of aggregations of the crown-of-thorns starfish, *Acanthaster planci* (L.). Nature 246(5429): 167-169. https://doi.org/10.1038/246167a0

Ortiz JC, Wolff NH, Anthony KR, Devlin M, Lewis S, Mumby PJ (2018) Impaired recovery of the Great Barrier Reef under cumulative stress. Science Advances 4(7): eaar6127. https://doi.org/10.1126/sciadv.aar6127

Pandolfi JM, Bradbury RH, Sala E, Hughes TP, Bjorndal KA, Cooke RG, McArdle D, McClenachan L, Newman MJ, Paredes G, Warner RR (2003) Global trajectories of the long-term decline of coral reef ecosystems. Science 301(5635): 955-958. 1 https://doi.org/10.1126/science.1085706

Pearson RG, 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.

Plagányi ÉE, Babcock RC, Rogers J, Bonin M, Morello EB (2020) Ecological analyses to inform management targets for the culling of crown-of-thorns starfish to prevent coral decline. Coral Reefs 39(5): 1483-1499.Plass-Johnson JG, Schwieder H, Heiden J, Weiand L, Wild C, Jompa J, Ferse SC, Teichberg M (2015) A recent outbreak of crown-of-thorns starfish (*Acanthaster planci*) in the Spermonde Archipelago, Indonesia. Regional Environmental Change 15(6): 1157-1162. https://doi.org/10.1007/s10113-015-0821-2

Potts DC (1981) Crown-of-thorns starfish - man-induced pest or natural phenomenon? Pages 55-86. In: Kitching RL, Jones RE (eds) The Ecology of Pests – Some Australian Case Histories, CSIRO Publishing, Melbourne.

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

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

Pratchett MS, Cumming GS (2019) Managing cross-scale dynamics in marine conservation: pest irruptions and lessons from culling of crown-of-thorns starfish (*Acanthaster* spp.). Biological Conservation 238: 108211. https://doi.org/10.1016/j.biocon.2019.108211

Pratchett MS, Schenk TJ, Baine M, Syms C, Baird AH (2009) Selective coral mortality associated with outbreaks of *Acanthaster planci* L. in Bootless Bay, Papua New Guinea. Marine Environmental Research 67(4-5): 230-236. https://doi.org/10.1016/j.marenvres.2009.03.001

Pratchett MS, Caballes CF, Rivera-Posada JA, Sweatman HPA (2014) Limits to understanding and managing outbreaks of crown-of-thorns starfish (*Acanthaster* spp.). Oceanography and Marine Biology: An Annual Review 52: 133–200.

Pratchett MS, Caballes CF, Wilmes JC, Matthews SA, Mellin C, Sweatman HPA, Nadler LE, Brodie JE, Thompson CA, Hoey J, Bos AR, Byrne M, Messmer V, Fortunato SAV, Chen CCM, Buck ACE, Babcock RC, Uthicke S (2017) Thirty years of research on crown-of-thorns starfish (1986-2016): Scientific advances and emerging opportunities. Diversity 9: 41. https://doi.org/10.3390/d9040041

Pratchett MS, Caballes CF, Cvitanovic C, Raymundo ML, Babcock RC, Doherty PJ, Doll PC, Doyle JR, Dworjanyn SA, Fabricius KE, Haywood MDE, Hock K, Hoggett A, Høj L, Keesing JK, Kenchington RA, Lang BJ, Ling SD, Matthews SA, McCallum HI, Mellin C, Mos B, Motti CA, Mumby PJ, Stump RJW, Uthicke S, Vail L, Wolfe K, Wilson SK (2021a) Knowledge gaps in the biology, ecology and management of pacific crown-of-thorns starfish, *Acanthaster* cf. *solaris*, on Australia's Great Barrier Reef. Biological Bulletin 241(3):330-346. ttps://doi.org/10.1086/717026

Pratchett MS, Nadler LE, Burn D, Lang BJ, Messmer V, Caballes CF (2021b) Reproductive investment and fecundity of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) on the Great Barrier Reef. Marine Biology 168(6): 87. https://doi.org/10.1007/s00227-021-03897-w

Pratchett MS, Caballes CF, Burn D, Doll PC, Chandler JF, Doyle JR, Uthicke S (2022) Scooter-assisted large area diver-based (SALAD) visual surveys to test for renewed outbreaks of crown-of-thorns starfish (*Acanthaster* cf. *solaris*) in the northern Great Barrier Reef. A report to the Australian Government by the COTS Control Innovation Program (32 pp). https://www.barrierreef.org/uploads/CCIP-EIP-02-Early-Investment-Project-COTS-Surveys-Final-Report.pdf

Pratchett MS, Chandler JF, Choukroun SM, Doll PC, Lang BJ, Kwong S, Chen CC, Emslie MJ, Caballes CF, Uthicke S, Matthews SA (2024) Biophysical processes involved in the initiation and spread of population irruptions of crown-of-thorns starfish on the Great Barrier Reef. Pages 290-305. In: Wolanski E, Kingsford MH (eds) Oceanographic Processes of Coral Reefs, CRC Press, Boca Raton.

Pratchett MS, Chandler JF, Figueira W, Dubuc A, Caballes CF, Doll PC (2025) Spatiotemporal variation in feeding behaviour of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*), including highly resolved estimated of daily consumption rates. A report to the Australian Government by the COTS Control Innovation Program.

Reichelt RE, Bradbury RH, Moran PJ (1990) Distribution of *Acanthaster planci* outbreaks on the Great Barrier Reef between 1966 and 1989. Coral Reefs 9(3): 97-103. https://doi.org/10.1007/BF00258219

Ripley B, Venables B, Bates DM, Hornik K, Gebhardt A, Firth D, Ripley MB (2013) Package 'mass'. Cran r. 538: 113-20.

Rogers JGD, Pláganyi ÉE, Babcock RC (2017) Aggregation, Allee effects and critical thresholds for the management of the crown-of-thorns starfish *Acanthaster planci*. Marine Ecology Progress Series 578: 99-114. https://doi.org/10.3354/meps12252

Stump R (1996) An investigation to describe the population dynamics of *Acanthaster planci* (L.) around Lizard Island, Cairns section, Great Barrier Reef Marine Park. CRC Reef Research Centre, Townsville.

Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. Current Biology 18(14): R598-599. https://doi.org/10.1016/j.cub.2008.05.033

Sweatman H, Bass DK, Cheal AJ, Coleman G, Miller IR, Ninio R, Osborne K, Oxley WG, Ryan DAJ, Thompson AA, Tomkins P (1998) Long-term Monitoring of the Great Barrier Reef. Status Report Number 3. Australian Institute of Marine Science, Townsville. https://www.aims.gov.au/sites/default/files/status-report-03.pdf

Trapon ML, Pratchett MS, Penin L (2011) Comparative effects of different disturbances in coral reef habitats in Moorea, French Polynesia. Journal of Marine Biology 2011: 807625. https://doi.org/10.1155/2011/807625

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. https://doi.org/10.1890/07-2136.1

Uthicke S, Pratchett MS, Bronstein O, Alvarado JJ, Wörheide G (2024a) The crown-of-thorns seastar species complex: knowledge on the biology and ecology of five corallivorous *Acanthaster* species. Marine Biology 171(1): 32. https://doi.org/10.1007/s00227-023-04355-5

Uthicke S, Doyle JR, Gomez Cabrera M, Patel F, McLatchie MJ, Doll PC, Chandler JF, Pratchett MS (2024b) eDNA monitoring detects new outbreak wave of corallivorous seastar (*Acanthaster* cf. *solaris*) at Lizard Island, Great Barrier Reef. Coral Reefs https://doi.org/10.1007/s00338-024-02506-8

Uthicke S, Gomez Cabrera M, Patel F, Lawrence E, Tabor B, Foster S, Doyle J (2025) Operationalising and implementing crown-of-thorns starfish (COTS) eDNA monitoring on the GBR. A report to the Australian Government by the COTS Control Innovation Program.

Uthicke S, Lamare M, Doyle JR (2018) eDNA detection of corallivorous seastar (*Acanthaster* cf. *solaris*) outbreaks on the Great Barrier Reef using digital droplet PCR. Coral Reefs 37(4): 1229-1239.

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

Vine PJ (1973) Crown of thorns (*Acanthaster planci*) plagues: the natural causes theory. Atoll Research Bulletin. 1973: 1-13.

Weber JN, Woodhead PMJ (1970) Ecological studies of the coral predator *Acanthaster planci* in the South Pacific. Marine Biology 6(1): 12-17. https://doi.org/10.1007/BF00352602

Westcott DA, Fletcher CS, Kroon FJ, Babcock RC, Plagányi EE, Pratchett MS, Bonin MC (2020) Relative efficacy of three approaches to mitigate crown-of-thorns starfish outbreaks on Australia’s Great Barrier Reef. Scientific Reports 10(1):12594. https://doi.org/10.1038/s41598-020-69466-1

Wilson SK, Graham NA, Polunin NV (2007) Appraisal of visual assessments of habitat complexity and benthic composition on coral reefs. Marine Biology 151(3): 1069-1076. https://doi.org/10.1007/s00227-006-0538-3

Wolanski E, Lambrechts J (2020) The net water circulation in the far Northern Great Barrier Reef. Estuarine, Coastal and Shelf Science 235:106569. https://doi.org/10.1016/j.ecss.2019.106569

Wooldridge SA, Brodie JE (2015) Environmental triggers for primary outbreaks of crown-of-thorns starfish on the Great Barrier Reef, Australia. Marine Pollution Bulletin 101(2): 805-815. https://doi.org/10.1016/j.marpolbul.2015.08.049

Wörheide G, Kaltenbacher E, Cowan Z-L, Haszprunar G (2022) A new species of crown-of-thorns sea star, *Acanthaster benziei* sp. nov. (Valvatida: Acanthasteridae), from the Red Sea. Zootaxa 5209: 379-393. https://doi.org/10.11646/ZOOTAXA.5209.3.7

Zann L, Brodie J, Vuki V (1990) History and dynamics of the crown-of-thorns starfish Acanthaster planci (L.) in the Suva area, Fiji. Coral Reefs 9(3):135-144. https://doi.org/10.1007/BF00258225

APPENDIX A

Table 3. Comparison of alternative models (GLMM) to test for spatiotemporal variation in abundance of COTS. Rather than test for variation in densities, we compared the total number of COTS and sets of scars recorded on each SALAD survey and then used the area sampled as an offset (e.g. Total ~ Region + (1|Reef) + offset(log(Area)), family = negative-binomial). All models also included a random effect for reef. Probabilities (*p*), based on chi-square test of model deviance, are presented to indicate significance of the final model.

			Model deviance		
Model	df	AICc	Deviance	df	p
Total ~ Region + (1 | ReefNo)	5	29,001.0			
Total ~ Region*Year + (1 | ReefNo)	9	28,196.4			
Total ~ Region*Coral + (1 | ReefNo)	9	26,027.9			
Total ~ Region*Zone + (1 | ReefNo)	11	28,876.9			
Total ~ Region*Year*Zone + (1 | ReefNo)	21	27,881.1			
Total ~ Region*Year+Coral + (1 | ReefNo)	17	25,293.2	2,446	8	<0.001

Table 4. Comparison of alternative models (GLMM) to test for spatiotemporal variation in detectability of COTS, using binomial distributions and a logit link functions (e.g. Detected ~ Region + (1|Reef), family = binomial (link="logit"). All models also included a random effect for reef. Probabilities (*p*), based on chi-square test of model deviance, are presented to indicate significance of the final model.

			Model deviance		
Model	df	AICc	Deviance	df	p
Detect ~ Region + (1 | ReefNo)	4	776.5			
Detect ~ Region*Inferred + (1 | ReefNo)	8	774.8			
Detect ~ Region*Complexity + (1 | ReefNo)	36	808.4			
Detect ~ Region*Coral + (1 | ReefNo)	8	692.7	27.9	7	<0.001
Detect ~ Region*Zone + (1 | ReefNo)	10	777.8			
Detect ~ Region*Year + (1 | ReefNo)	8	799.1			
Detect ~ Region*Year*Inferred	16	775.6			

Table 5. Comparison of alternative models (GLMM) to test for spatiotemporal variation in exposure of COTS that were sighted during SALAD surveys, using binomial distributions and a logit link functions (e.g. Exposed ~ Region +

(1|Reef), family = binomial (link="logit")). All models also included a random effect for reef. Probabilities (*p*), based on chi-square test of model deviance, are presented to indicate significance of the final model.

			Model deviance		
Model	df	AICc	Deviance	df	p
Exposed ~ Region + (1 | ReefNo)	5	1,515.7			
Exposed ~ Region*Year + (1 | ReefNo)	9	1,518.1			
Exposed ~ Region+Size + (1 | ReefNo)	6	1,486.3	238	4	<0.001
Exposed ~ Region*Year+Size + (1 | ReefNo)	10	1,492.4	239	8	<0.001

Table 6. Comparison of alternative models (GLMM) to test for spatiotemporal variation in coral cover, using binomial distributions and a logit link functions (e.g. Coral ~ Region + (1|Reef), family = binomial (link="logit"). All models also included a random effect for reef. Probabilities (*p*), based on chi-square test of model deviance, are presented to indicate significance of the final model.

			Model deviance		
Model	df	AICc	Deviance	df	p
Coral ~ Region + (1 | ReefNo)	4	632.3			
Coral ~ Region*Year + (1 | ReefNo)	8	633.9			
Coral ~ Region+Inferred + (1 | ReefNo)	5	627.4	18.1	4	0.002
Coral ~ Region*Year+Inferred+ (1 | ReefNo)	9	628.8			

Morgan S. Pratchett (morgan.pratchett@jcu.edu.au)
Marine Biology, College of Science and Engineering,
James Cook University, Townsville, Queensland 4811

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

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