#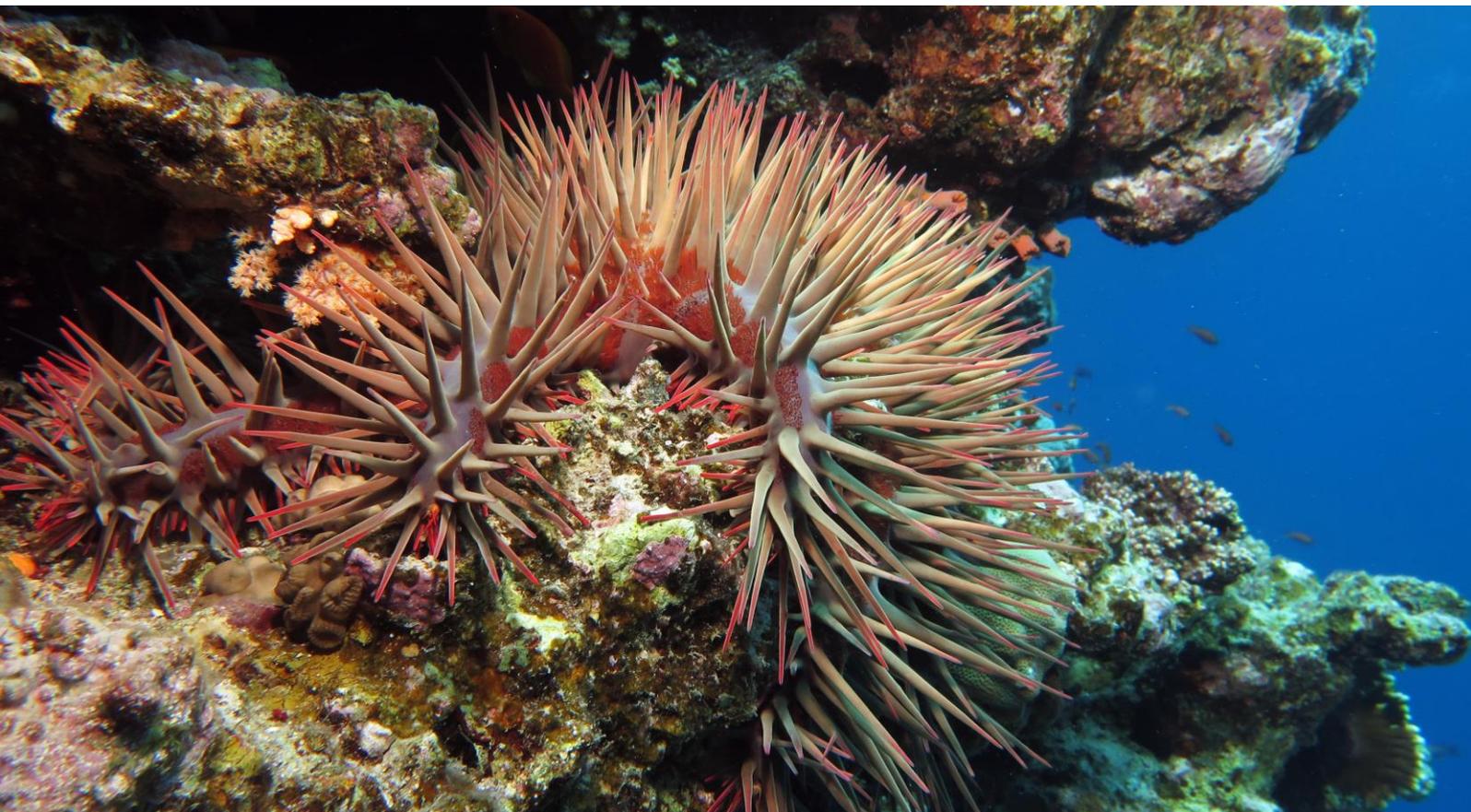 Scooter-assisted large area diver-based (SALAD) visual surveys to test for renewed outbreaks of crown-of-thorns starfish (Acanthaster cf. solaris) in the northern Great Barrier Reef Report title

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

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

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

1. ARC Centre of Excellence for Coral Reef Studies, James Cook University
2. Australian Institute of Marine Science

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Acronyms and Abbreviations

CoTS	Crown-of-Thorns Starfish
ddPCR	Digital Droplet Polymerase Chain Reaction
GBR	Great Barrier Reef
LOD	Limit of Detection
LOQ	Limit of Quantification
SALAD surveys	Scooter-Assisted Large Area Diver-based visual surveys

EXECUTIVE SUMMARY

Successive reef-wide population irruptions of CoTS on Australia's Great Barrier Reef (GBR) are purported to have started on reefs between Lizard Island (14.6°S) and Cairns (17°S). Accordingly, this area has come to be known as the *initiation box*, and much of the research on CoTS aimed at addressing the cause(s) of population irruptions is concentrated in this area. However, in some previous outbreaks there were detectable increases in the abundance of adult CoTS in the far northern GBR well ahead of similar reports for reefs (e.g., Lizard Island) within the putative *initiation box*. This study uses relatively new and novel sampling methods to explore the current densities of CoTS in the northern GBR, and specifically test for elevated (albeit potentially very moderate) densities of CoTS that might represent the precursor of impending population irruptions.

Effectively sampling low-density populations of crown-of-thorns starfish (CoTS) necessitates surveying large areas of reef habitat, which has traditionally been achieved using manta-tow methods. However, manta-tow surveys have limited capacity to detect CoTS, which are mostly concealed beneath corals or within the reef matrix. Conversely, intensive visual surveys greatly increase the detection of CoTS, but are inherently limited in their spatial extent. In this study, we used underwater scooters to substantially increase the spatial extent of visual surveys undertaken by SCUBA divers, but without constraining the capacity to stop and search for CoTS within complex reef habitats, and whenever feedings scars are observed.

In 2021, a total of 90 scooter-assisted large area diver-based (SALAD) visual surveys were conducted across 14 reefs in 4 distinct regions, encompassing a combined survey area of 46.39 hectares. Recorded densities of CoTS were substantially higher in the Cape Grenville Region (25.17 CoTS.ha^{-1} ±4.45SE) compared to the Princess Charlotte Bay Region (7.91 CoTS.ha^{-1} ±1.78SE), the Lizard Island Region (7.41 CoTS.ha^{-1} ±1.36SE) and the Cairns Region (9.99 CoTS.ha^{-1} ±1.42SE). CoTS densities also varied among the 3-4 reefs surveyed within each region, with the highest densities recorded at McSweeney Reef (43.98 CoTS.ha^{-1} ±6.65SE) and U/N 11-049 (24.04 CoTS.ha^{-1} ±4.27SE) in the Cape Grenville Region. At all other reefs mean densities recorded were <15 CoTS.ha^{-1}.

Aside from elevated densities of CoTS recorded in the Cape Grenville Region, the mean size (diameter) of CoTS recorded in the Cape Grenville Region (43.51 cm ±0.72SE) was substantially higher than recorded in the Princess Charlotte Bay Region (25.00 cm ±2.24SE), the Lizard Island Region (34.89 cm ±1.25SE) and Cairns Region (24.85 cm ±1.76SE). Large CoTS (>50 cm diameter) were almost exclusively recorded in the Cape Grenville Region, and accounted for 21.2% (22 out of 104) of CoTS recorded in this region. In contrast, CoTS populations in the Princess Charlotte Bay Region and the Cairns Region were dominated by small individuals (10-20cm diameter).

A key issue in the application of survey data for improved understanding and management of population irruptions is the limited detectability of CoTS in coral reef environments. Accordingly, we compared the recorded incidence of distinct sets of feeding scars with the actual number of CoTS detected along each individual survey path, as a proxy for detectability. Based on these data, detectability was much higher in the Cape Grenville Region (66.6% ±5.67SE) and the Lizard Island Region (55.2% ±6.39SE), compared to the Princess Charlotte Bay Region (30.7% ±8.11SE) and the Cairns Region (30.0% ±6.25SE). These differences appear to reflect regional

differences in the size of CoTS. However, there was no relationship between detectability and CoTS densities.

Complementary sampling to estimate local occurrence and abundance of CoTS, using both diver-based (scooter-assisted large area diver-based visual surveys) and diver-independent (eDNA) methods, has revealed general concordance across complementary sampling methods, at least at the scale of individual reefs. eDNA sampling detected CoTS in all reefs and regions surveyed, though levels of detection (based on the proportion of samples in which CoTs were detected) varied among reefs, ranging from 5% to 90%. These data demonstrate that capacity of scooter-assisted large area diver-based visual surveys to effectively detect CoTS, even at very low densities.

This study shows that there are elevated densities of CoTS on reefs in the far northern GBR (mainly at reefs off Cape Grenville), which may be an important precursor to impending reef-wide population irruptions. This finding reaffirms results from previous analyses showing that during previous population irruptions of CoTS on the GBR (in the 1990s), there were detectable increases in the abundance of adult CoTS in the far northern GBR well ahead of similar reports for reefs (e.g., Lizard Island) within the putative *initiation box*. Ongoing and extensive sampling is therefore, needed across the broader extent of the northern and far northern GBR to maximise the early detection of renewed population irruptions, and thereby contribute to improved understanding of the cause(s) and management of these phenomena.

1.   INTRODUCTION

1.1 The Crown-of-thorns Starfish (*Acanthaster* spp.)

Crown-of-thorns starfish (CoTS; *Acanthaster* spp.) are among the most intensively studied coral reef organisms (Moran 1986, Pratchett et al. 2017), partly due to marked spatiotemporal variation in their abundance (e.g., Chesher 1969, Reichelt et al. 1990, Kayal et al. 2012). Most notably, there appear to be two distinct modalities of CoTS populations, whereby on most reefs and for most of the time CoTS are virtually undetectable and their densities are considered negligible (Weber & Woodhed 1970, Moran 1986, Fernandes et al. 1992). Conversely, extremely high densities of CoTS (>1,500 individuals.ha^{-1}; Kayal et al. 2012) have been recorded during periodic population irruptions (also referred to as outbreaks; Birkeland 1982). Population irruptions of CoTS have been recorded throughout the Indo-Pacific, from the Red Sea (Ormond et al. 1973) to Hawaii (Kenyon & 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).

Population irruptions of CoTS are variously attributed to either their inherent life history characteristics (mainly their exceptional fecundity; Moore 1978, Uthicke et al. 2009), versus anthropogenic or environmental changes that have potentially disrupted ecological processes that otherwise regulate CoTS populations (e.g., Brodie et al. 2005, Sweatman 2008, Fabricius et al. 2010, Kroon et al. 2021). In reality, it is likely that population irruptions of CoTS result from a multitude of factors (e.g., Babcock et al. 2016, Pratchett & Cumming 2019), whereby pervasive effects of humans on coastal ecosystems are likely to have fundamentally altered the structure and function of CoTS populations and reef ecosystems (Pratchett et al. 2014). However, there is limited data on changes in population demographics of CoTS coinciding with the initiation or establishment of population irruptions, which would help to resolve the relative importance of intrinsic versus extrinsic processes (MacNeil et al. 2017). This is because CoTS studies are generally initiated only after population irruptions are established (e.g., Chesher 1969), and demographic information for CoTS is largely limited to estimates of abundance and size structure.

Acanthaster spp. have gained considerable notoriety, not only because of their tendency to undergo rapid and dramatic increases in abundance, but because population irruptions contribute greatly to coral loss and reef degradation (e.g., Chesher 1969, Kayal et al. 2012). Population irruptions of CoTS have long been considered one of the major causes of coral loss throughout the Indo-Pacific (e.g., Pearson 1981, Bruno & Selig 2007, De'ath et al. 2012), and their ecological impacts are increasingly being compounded by other major disturbances, such as climate-induced coral bleaching (e.g., Trapon et al. 2011, Mellin et al. 2019). The cumulative effects of these disturbances, along with chronic pressures (e.g., declining water quality), have caused sustained and accelerating degradation of coral reef ecosystems in many regions of the Indo-Pacific (e.g., Bruno & Selig 2007, Bellwood et al. 2019, Bauman et al. 2021) and represent a significant challenge for coral reef management and conservation.

Crown-of-thorns starfish occur on coral reefs throughout the Indo-Pacific, with at least four distinct and largely sympatric species occurring in different reef regions (Haszprunar et al. 2017). While all *Acanthaster* spp. recorded in shallow water habitats were previously regarded to be *Acanthaster planci* (e.g., Moran 1986, Pratchett et al. 2014), *A. planci* is now known to be restricted to the northern Indian ocean (Haszprunar et al. 2017) and is readily distinguishable

from the western Pacific species, *Acanthaster* cf. *solaris* (Pratchett et al. 2017). Most of the scientific research on CoTS has been undertaken on Australia's Great Barrier Reef (GBR) and elsewhere in the western Pacific (e.g., Japan), thus on *Acanthaster* cf. *solaris* (Pratchett et al. 2017).

1.2 Population Irruptions of Crown-of-thorns Starfish on the Great Barrier Reef

The first documented population irruptions of CoTS (*Acanthaster* cf. *solaris*) on the GBR occurred in the early 1960s (Pearson & Endean 1969), though there are anecdotal reports of high densities of CoTS on the GBR much earlier (Vine 1973, Ganter 1987). Since the 1960s, there have been three additional distinct episodes of population irruptions on the GBR, commencing in approximately 1979, 1993, and 2009 (Pratchett et al. 2014). The initiation and progression of the first two documented population irruptions, based on extensive but largely uncoordinated sampling across the GBR, appears to have been very similar (Kenchington 1977, Moran 1986, Reichelt et al. 1990). Most notably, Kenchington (1977) suggested that population irruptions started in the northern GBR and then propagated southwards via relatively localised dispersal of larvae. Sequential progression of population irruptions thereby occurred as each distinct population matured, spawned, and then further contributed to the production of larvae, which in turn colonised reefs even further south (Kenchington 1977). Kenchington's (1977) hypothesis regarding the southerly spread of outbreaks was based on re-analyses of size-frequency distributions from several distinct reefs during the first documented population irruptions, and was later confirmed by detailed data on the spatiotemporal occurrence of population irruptions at individual reefs along the GBR (Reichelt et al. 1990, Vanhatalo et al. 2017). However, systematic monitoring to document spatiotemporal patterns of population irruptions commenced in the 1980s, after the second documented irruptive event was already well underway (Moran et al. 1988, Sweatman et al. 2011).

Each of the four documented population irruptions of CoTS on the GBR are purported to have started on mid-shelf reefs between Lizard Island (14.6ºS) and Cairns (17ºS), which has come to be known as the *initiation box* (Figure 1.1). In the early 1960s and late 1970s, high densities of CoTS were first detected (or at least reported) on reefs (e.g., Green Island) close to Cairns (Pearson & Endean 1969, Kenchington & Pearson 1982), though this is also where the probability of detecting elevated CoTS densities was likely highest. It was acknowledged therefore, that population irruptions likely originated on reefs north of Cairns (Reichelt et al. 1990). In the 1990s and 2000s (at the start of the third and fourth documented population irruptions), high densities of CoTS were first recorded in the northernmost section of the initiation box, in the vicinity of Lizard Island (Sweatman et al. 1998, Pratchett 2005, but see Wooldridge & Brodie 2015), though population irruptions were quickly apparent on reefs throughout the *initiation box* (Harrison et al. 2017).

Despite extensive monitoring for CoTS, it is not viable to survey all reefs (~3,000) across the vast expanse of the GBR, and even the regularly surveyed reefs are generally only surveyed once every 2 years (Mellin et al. 2020). This, combined with limited capacity to detect CoTS at very low densities, has greatly constrained improvements in understanding of when and where population irruptions of CoTS actually start, fuelling persistent controversies regarding the cause(s) of population irruptions (Babcock et al. 2016). Recent research into putative causes of population irruptions of CoTS has focussed on reefs in the broadly designated *initiation box*, in either the Lizard Island Region (Pratchett 2005) and/ or the Cairns Region (Wooldridge & Brodie 2015,

Harrison et al. 2017, MacNeil et al. 2017). It is possible however, that populations irruptions may originate on reefs at even lower latitudes, in Princess Charlotte Bay or off Cape Grenville (e.g., Vanhatalo et al. 2017), and that proliferation of CoTS at reefs in the Lizard Island region is due to the secondary accumulation of extensive larvae spawned by established CoTS populations at reefs to the north. This idea has not previously been given serious consideration, largely because prevailing currents are generally understood to flow northwards from the Lizard Island Region and up through Princess Charlotte Bay (e.g., Fabricius et al. 2010). Even if oceanographic influences and prevailing currents are weak in the far northern GBR, there is expected to be very limited connectivity between these reefs and reefs to the south (Wolanski & Lambrechts 2020). However, during previous population irruptions, Vanhatalo et al. (2017) showed that elevated densities of adult CoTS were apparent in the far northern GBR (around 12° of latitude) up to 2-years before population irruptions were detected at reefs within the purported *initiation box* (e.g., Lizard Island).

1.3 Objectives

This purpose of this study was to test the utility of a relatively new and novel sampling method (scooter-assisted large area diver-based (SALAD) visual surveys) and explore the current densities of CoTS in the northern GBR. The location and timing of the sampling was specifically intended to test for elevated (albeit potentially very moderate) densities of CoTS that might represent the precursor of impending population irruptions. Effectively sampling low-density populations of crown-of-thorns starfish necessitates surveying large areas of reef habitat, which has traditionally been achieved using towed-diver (e.g., Kenyon & Aeby 2009) or manta-tow methods (e.g., Vanhatalo et al. 2017). However, such methods generally only record the limited number of CoTS that are highly exposed and readily visible from above (Fernandes et al. 1990), with limited capacity to detect CoTS that are often concealed beneath corals or within the reef matrix. Conversely, intensive visual surveys undertaken by autonomous divers (e.g., Pratchett 2005, Kenyon & 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).

In this study, SALAD surveys were undertaken at select reefs within the area known as the *initiation box* in the northern Great Barrier Reef (extending from Cairns to Cooktown), with complementary sampling at reefs in Princess Charlotte Bay and north to Cape Grenville (Figure 1.1). These two areas are well-north of the generally reported *initiation box* (e.g., Fabricius et al. 2010), based on previous observation by Vanhatalo et al. (2017). Recent broad-scale surveys undertaken by the Australian Institute of Marine Science also reported an incipient outbreak of CoTS at one reef (Unnamed Reef U/N 11-049) off Cape Grenville (www.aims.gov.au/reef-monitoring/cape-grenville-sector-2021).

A key objective of this research is to provide a platform for monitoring CoTS populations ahead of renewed population irruptions on the GBR, expected to occur by 2025 (Babcock et al. 2020), thereby providing an unprecedented information on changes in the distribution and abundance of CoTS during the initiation of population irruptions. Understanding when and where reef-wide population irruptions start will not only help to identify potential triggers or causes of population irruptions, but increase the window of opportunity in which to act to prevent (or at least contain) future population irruptions. Accordingly, surveys reported in this study will be undertaken annually to assess spatiotemporal changes in the distribution and abundance of CoTS from 2021 until 2024.

1.4 Previous sampling

Sampling undertaken for this study (in 2021) also builds on complementary sampling that was initiated in 2019. Initial sampling was undertaken at Lizard Island with the goal of developing a survey method capable of detecting and effectively quantifying densities of CoTS at low densities. Sampling was later expanded to include reefs off Cairns, mainly to assess the relative timing of the initiation of impending population irruptions in the northern (Lizard Island Region) versus southern section of the putative *initiation box* (Cairns Region). These data, therefore, provide insights on recent changes in the abundance of CoTS, especially at Lizard Island where, despite ongoing culling effort, there were increases in CoTS densities from 2019 to 2021.
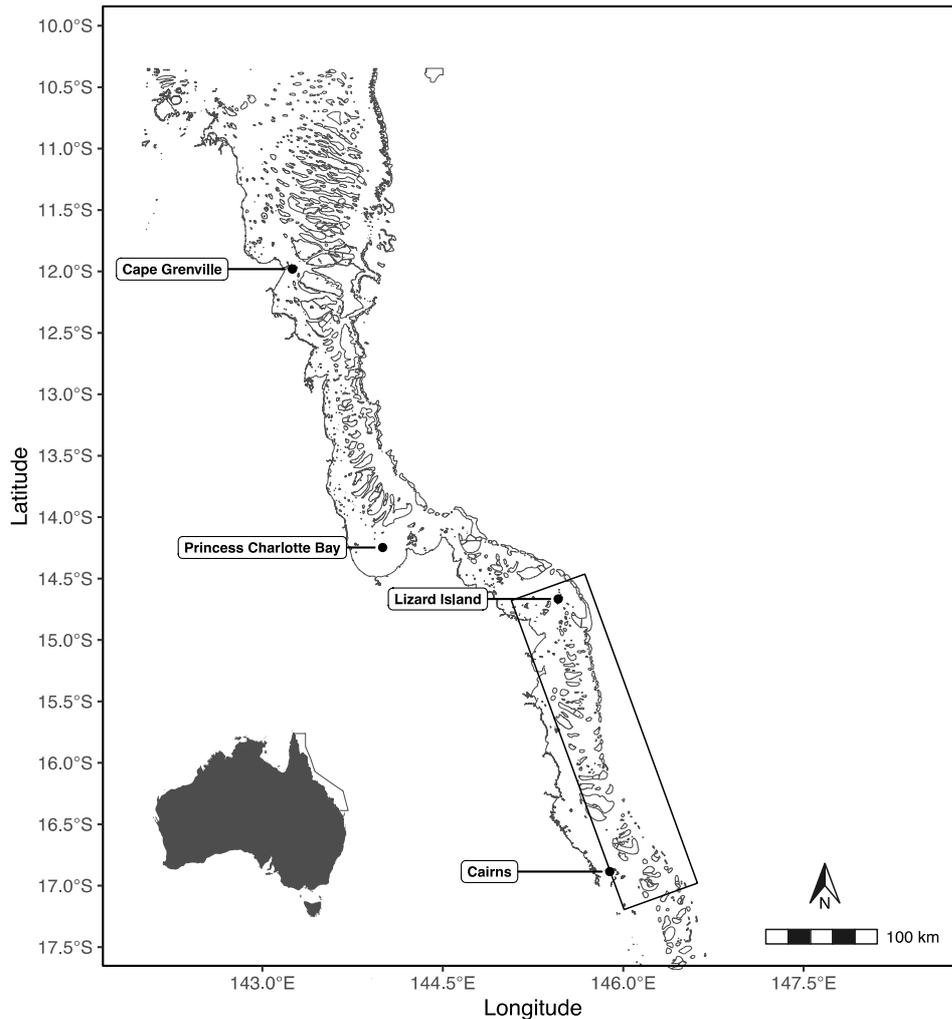
Figure 1.1. Map of the northern Great Barrier Reef, showing the putative initiation box, where population irruptions of western Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) are reported to originate. Labels indicate four distinct regions where sampling was undertaken to test for variation in the size and abundance of crown-of-thorns starfish in 2021.

2. METHODS

Effective sampling of low-density, non-outbreaking CoTS populations is fundamental in assessing changes in their behaviour and biology during the initiation of population irruptions. This project utilises a tractable and viable method for sampling low-density population of crown-of-thorns starfish; scooter-assisted large area diver-based (SALAD) visual surveys. This method which has been developed during the last 3 years, builds on the demonstrated utility of transect-based visual surveys (typically 50 m x 5 m) and high levels of detectability that are achieved by autonomous divers (e.g., Pratchett 2005), while greatly increasing the areal extent of surveys to account for the inherent patchiness in the abundance of CoTS. The utility of SALAD surveys is also being tested by comparing detectability of CoTS against diver-independent sampling methods that use environmental DNA (eDNA) to record the local presence of adult CoTS (e.g., Uthicke et al. 2018).

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

SALAD surveys were undertaken using Yamaha (500Li) Seascooters. These underwater scooters greatly increased the area that could be surveyed, while allowing complete autonomy over the direction and speed of movement. Most notably, the speed of movement varied in accordance with visibility and habitat complexity to maximise detection of CoTS.

During each scooter survey, divers would traverse a section of reef searching for feeding scars and CoTS within a 5-m wide belt. Divers worked in pairs, but independently surveyed distinct habitats 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 varied according to visibility and habitat structure.

Where practicable, divers were attached to a surface float that housed a small, waterproof GPS unit. Aside from recording GPS co-ordinates for the start and end of each surveyed track, GPS co-ordinates were recorded at 30 second intervals to provide a detailed record of the pathway taken by each diver. These data were used to determine the distance travelled by each diver and the overall search area, necessary to estimate the local densities of CoTS.

Multiple distinct SALAD surveys were undertaken at each reef, whereby each survey represented the extensive searching of a prescribed area of reef by a single researcher and during a single dive (averaging 67.85 minutes duration $\pm$1.3SE). Most scooter surveys were conducted along continuous reef margins, whereby researchers gradually progressed along the reef contour throughout the course of the survey. However, some surveys were conducted on distinct patch reefs, where the divers carefully searched the entire circumference of the reef and terminated the survey when they returned to the starting point.

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). Whenever divers located a feeding scar, but were unable to locate any CoTS within the local area, the scar was carefully inspected to rule out tissue loss due to coral disease or *Drupella* spp. Where confident the tissue loss was caused by CoTS, it was assumed that the CoTS responsible was located in the local vicinity, but not detectable. The number of distinct 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 estimate CoTS densities for each survey area.

In 2021, a total of 90 scooter surveys were conducted across 14 reefs and 4 distinct regions, with a combined survey area of 463,925m², or 46.39 hectares (Table 2.1). The *a priori* goal was to complete at least 6 surveys at each reef, though this was not possible at MacGillivray Reef, Eagle Island, nor North Direction Island, owing to poor weather and limited sampling opportunities in 2021. The total area surveyed at these reefs (>22,000m²) was however, comparable to the areal extent of surveys completed at other reefs (Table 2.1), given the large areal extent of surveys at these reefs.

Table 2.1. Number and areal extent of scooter-assisted large area diver-based visual surveys used to assess the distribution and abundance of CoTS across the northern GBR in 2021. The length and therefore areal extent of individual surveys vary with habitat, conditions and CoTS densities. The combined area of all surveys conducted at each reef (which ranges from 2-22) is provided.

Region	Reef/ Island	n	Combined Area (m²)
Cape Grenville	McSweeney	6	24,170
	U/N 11-049	6	23,285
	U/N 11-162	6	19,710
Princess Charlotte Bay	Corbett	6	30,755
	U/N 13-040	6	24,235
	U/N 13-124	6	23,210
	Davie	6	21,040
Lizard Island	Lizard Island	22	159,915
	MacGillvray	2	22,105
	Eagle	2	23,425
	North Direction	4	24,720
Cairns	Thetford	6	18,540
	Moore	6	22,980
	Elford	6	25,835
Total		90	463,925

The aforementioned surveys add to complementary surveys initiated in 2019. Over the period from 2019 to 2021, a total of 264 scooter-assisted large area diver-based visual surveys have been conducted in the northern and central GBR, with recurrent sampling over multiple years at several reefs in the Lizard Island Region (2019-2021) and the Cairns Region (2020-2021). The majority of scooter surveys conducted throughout the extended sampling period have been conducted in the Lizard Island Region, and especially Lizard Island itself (96 surveys). At Lizard

Island, surveys were also conducted in the same general areas, and often the same exact sites, in successive years, providing unprecedented insights into temporal changes in the distribution and abundance of low-density CoTS populations.

2.2 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., Ficetola et al. 2008, Thomsen et al. 2012, Uthicke et al. 2018). Critically, eDNA sampling is not intended to sample individual organisms, but biological by-products, such as mucous and excrement (Thomsen & Willerslev 2015). 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 with active population irruptions. Rather than detecting when and where population irruptions occur, eDNA may have greatest utility in detecting the local presence or occurrence of CoTS on reefs with very limited densities (Doyle and Uthicke 2020, Uthicke et al. in review), though sampling intensity required to detect very low densities of CoTS will be higher than that needed to detect high densities of large adult CoTS.

To test for concordance between contrasting sampling methods, water samples have been taken for eDNA analyses at a total of 33 sites across the 10 reefs where scooter-assisted large area diver-based visual surveys have also been conducted (Table 2.2). To test this relations across a significant range of CoTS densities, sampling has been conducted at aforementioned regions of the northern GBR (Table 2.1), but also reefs in the Townsville region, at reefs with relatively high densities of CoTS. Where feasible, water samples were taken within close proximity (within 100m and generally downstream) of specific survey locations. However, 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 densities of CoTS derived using scooter-assisted large area diver-based to the proportion of filters at each reef, in which eDNA of CoTS was detected above accepted levels of detection (LOD).

Water samples were collected by directly filtering 2.5 L through a 1.2 mm mixed cellulose ester 47 mm filter membrane using a filtration cartridge sourced from Smith-Root (Cat # 10966) and an eDNA sampling device (Grover-Pro™) sourced from Grover Scientific Pty Ltd. The filter was carefully folded into eights and placed into a 1.5 ml screw cap tube followed by the addition of 540 ml of Qiagen buffer ATL as a preservation agent (Majaneva et al., 2018). Field control samples were conducted for each Reef by filtering 2.5 L freshwater. All equipment was cleaned between use by soaking for 30 minutes in concentrated pool chlorine solutions (100g dichloroisocyanuric acid 20 L^{-1}, equivalent to 0.275% w/v available chlorine). Samples were batched processed according to field trips. Samples were extracted using a Qiagen DNeasy kit on a Qiacube according to the manufacture's guidelines with the following exceptions: samples were incubated overnight (56°C) with shaking in Qiagen buffer ATL/proteinase K (540 µl/60 µl respectively); a 200 µl aliquot of this initial lysis was transferred to a new tube and 200 µl Qiagen buffer AL added (beginning of Qiacube automated extraction). This ATL/proteinase K/AL mixture was incubated at 56°C for 30 min with shaking; and the final elution was in 50 µl 10 mM Tris pH 8.0.

Samples were analysed via digital droplet PCR (ddPCR) as described in Uthicke et al. (2018) and run as technical duplicates. Quantitative determination of the CoTS mtDNA copy number uses the limit of quantification as described in Uthicke et al. (2018) and is a more conservative

threshold than the limit of detection. Consequently, a positive detection (ie. limit of detection (LOD)) was defined as one that contains a positive droplet count greater than the no template controls (NTC), negative extraction controls or field controls (Hunter et al., 2018). For a sample to be considered positive, either of the technical duplicates can be positive. Typically, controls do not contain any positive droplets and therefore any positive droplet count greater than zero is recorded as a positive detection. In the case of a positive droplet in controls, a false positive correction procedure is applied at the 'trip' (or batch) level as follows:

In the case of a positive droplet in controls (we never observed more that on droplet in a negative control), a false positive correction procedure is applied at the 'trip' (or batch) level as follows; i) Establish the mean false positive detection probability (± 95%CI) in control data (*number of control technical replicates having 1 droplet / total number of control technical replicates analysed*); ii) Multiply the mean false positive probability by the number of sample technical replicates assayed for each Reef to determine an estimated number of false positives expected at each Reef; iii) Randomly select the number determined from step 2) of positive (>0 droplets) ddPCR's from within a set of Reef samples and subtract a single positive droplet from each technical replicate randomly selected ddPCR result.

Table 2.2. Distribution and extent of eDNA sampling for CoTS, used to verify detectability of CoTS using scooter-assisted large area diver-based visual surveys.

Region	Reef (Year)	No. sites	No. samples (filters)
Cape Grenville	McSweeney (2021)	3	36
	U/N 11-049 (2021)	3	36
	U/N 11-162 (2021)	3	36
Princess Charlotte Bay	Corbett (2021)	3	36
	U/N 13-124 (2021)	3	36
	Davie (2021)	3	36
Lizard Island	Lizard Island (2020)	5	150
Cairns	Thetford (2020)	2	30
	Moore (2020)	2	30
	Elfiord (2020)	2	30
Townsville	Kelso (2020)	2	30
	Rib (2020)	2	30
Total		33	516

2.3 Data analyses

Data arising from scooter-assisted large area diver-based visual surveys not only includes independent density estimates obtained by carefully surveying very large discrete areas of reef habitat (2,715-12,250 m^2), but also important information on population structure (e.g., size structure) and behaviour. The primary purpose of this study was to test for variation in CoTS densities among and within the distinct reef regions; Cape Grenville Region, Princess Charlotte Bay Region, Lizard Island Region, and Cairns Region. To avoid confounding spatial contrasts

with inherent temporal dynamics in the distribution and abundance of CoTS (*sensu* Pratchett 2005), comparisons were conducted based solely on surveys conducted in 2021.

In 2021, size (diameter to nearest cm) was recorded for a total of 214 individual CoTS across the 4 regions; Cape Grenville Region (n = 104) Princess Charlotte Bay Region (n = 28), Lizard Island Region (n = 62), and Cairns Region (n= 20). Size could not be measured for all individuals recorded (n = 220), at least not without damaging coral habitat, because some individuals were detected deep within the reef matrix. To compare size structure of CoTS populations, data was pooled among reefs within regions, thereby testing for regional differences in size structure. Assuming that variation in the recorded size of CoTS corresponds with age (Kenchington 1977, MacNeil et al. 2017, but see Deaker et al. 2020), we would expect that CoTS would be generally larger in areas where increasing densities first occur, thereby providing potential insights into establishment and spread of population irruptions (*sensu* Kenchington 1977). Conversely, a preponderance of small CoTS (<20 cm diameter) may indicate areas where there have been significant and increasing levels of recruitment in recent years.

A key issue in the application of survey data for improved understanding and management of population irruptions is the limited detectability of CoTS in coral reef environments (MacNeil et al. 2016, Kayal et al. 2017). For relatively large CoTS, detectability may be as high as 82% (MacNeil et al. 2016, Kayal et al. 2017), though very few small starfish (especially, <10 cm diameter) are detected, even during intensive surveys in constrained areas. During field-based surveys, evidence of recent feeding activity (feeding scars) is often more prominent than the appearance of actual CoTS (e.g., Plass-Johnson et al. 2015). Therefore, we compare the recorded incidence of distinct sets of feeding scars with the actual number of CoTS detected along each individual survey path, as a proxy for detectability. Even accounting for feeding scars, it is likely that the local density of CoTS was underestimated, because it was necessarily assumed that distinct clusters of feeding scars were caused by a single CoTS, rather than the aggregated feeding by multiple CoTS. Moreover, not all CoTS will necessarily leave conspicuous evidence of recent feeding activity.

3. RESULTS

3.1 Distribution and abundance of CoTS in 2021

In 2021, we conducted a total of 90 scooter-assisted large area diver-based (SALAD) visual surveys, across 14 reefs and 4 regions (Table 2.1), with a combined search area of 46.39 hectares. A total of 220 CoTS, as well as a further 217 distinct feeding scars, were recorded across all surveys, resulting in an overall estimated density of 11.61 CoTS.ha^{-1} ($\pm$1.33SE). Mean densities recorded across replicate surveys were substantially higher in the Cape Grenville Region (25.17 CoTS.ha^{-1} $\pm$4.45SE) compared to the Princess Charlotte Bay Region (7.91 CoTS.ha^{-1} $\pm$1.78SE), the Lizard Island Region (7.41 CoTS.ha^{-1} $\pm$1.36SE) and the Cairns Region (9.99 CoTS.ha^{-1} $\pm$1.42SE). The proportion of surveys where CoTS were detected was 100% in the Cape Grenville Region (18 out of 18 surveys, with up to 21 CoTS recorded in a single survey) and Cairns Region (18 out of 18 surveys, with up to 11 CoTS recorded in a single survey), compared to 83.3% in the Princess Charlotte Bay Region (20 out of 24 surveys, with up to 19 CoTS recorded in a single survey) and Lizard Island Region (25 out of 30 surveys, with up to 12 CoTS recorded in a single survey). Mean, median and maxumum densities of CoTS were all substantially higher in the Cape Grenville Region, compared to the Princess Charlotte Bay Region, the Lizard Island Region, and the Cairns Region (Figure 3.1).
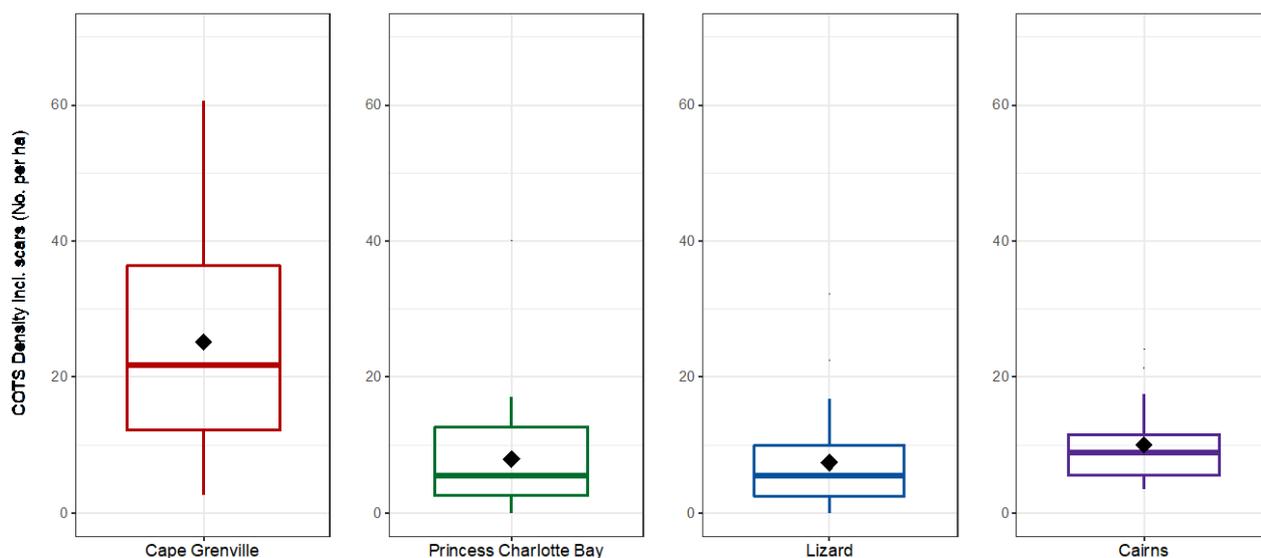
Figure 3.1. Box plots showing regional variation in CoTS densities in 2021 from the northern Great Barrier Reef. Each data point represents a single scooter-assisted large area diver-based visual survey. All data is presented as number of CoTS (including the number of distinct sets of feeding scars where CoTS were undetected) recorded per hectare. Black diamonds show the mean density recorded per region.

CoTS densities varied markedly among the 3-4 reefs surveyed within each region (Figure 3.2). Most notably, the densities of CoTS recorded at McSweeney Reef in the Cape Grenville Region (43.98 CoTS.ha^{-1} $\pm$6.65SE) were substantially higher than densities recorded at U/N 11-049 (24.04 CoTS.ha^{-1} $\pm$4.27SE) and U/N 11-162 (7.48 CoTS.ha^{-1} $\pm$2.51SE), in the same region. That said, CoTS densities recorded at McSweeney Reef and U/N 11-049 were the highest recorded across all 14 reefs across the 4 distinct regions (Figure 3.2); at all other reefs mean densities recorded were <15 individuals per hectare. CoTS were detected at virtually all reefs surveyed, with the exception of MacGillivray in the Lizard Island Region.

Surveys undertaken in 2021 within the Lizard Island Region were not evenly apportioned among the different reefs, where 22 out of 30 surveys were conducted at Lizard Island itself (Table 2.1). Relatively limited sampling was undertaken at other nearby reefs (Eagle Island, MacGillivray Reef and North Direction Island) owing to logistical constraints and bad weather. The total area surveyed was >22,000m^2 across all reefs, but given the apparent patchiness in the distribution and abundance of CoTS (as shown for Lizard Island, where densities ranged from 0 up to 32.25 CoTS.ha^{-1} among surveys), the resulting data does not necessarily reflect the status of CoTS populations at these other reefs.
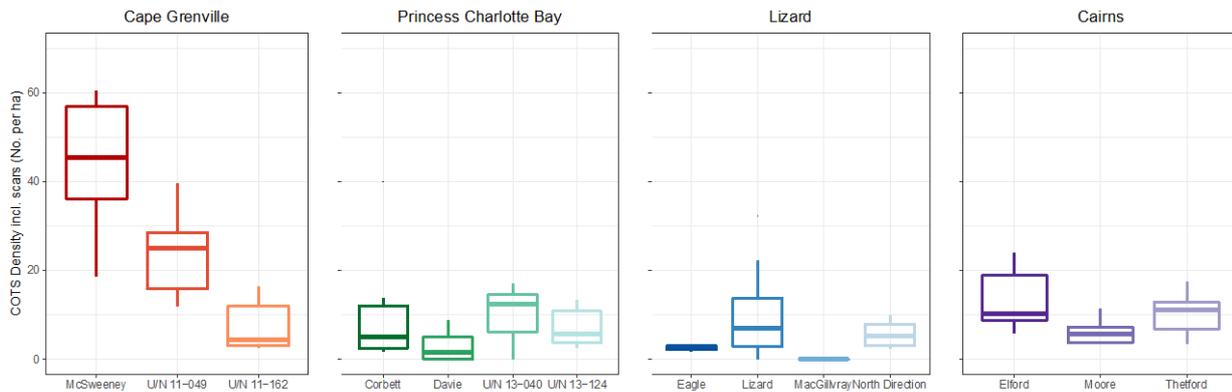
Figure 3.2. Box plots showing recorded densities of CoTS at each reef sampled within each of the four distinct regions. Each data point represents a single scooter-assisted large area diver-based visual survey. All data is presented as number of CoTS (including the number of distinct sets of feeding scars where CoTS were undetected) recorded per hectare.

3.2 Size structure of CoTS recorded in 2021

The size of CoTS recorded during scooter-assisted large area diver-based visual surveys in the northern GBR in 2021 (n = 214) ranged from 10 to 64 cm diameter. Larger CoTS (>50 cm diameter) were almost exclusively recorded in the Cape Grenville Region, and accounted for 21.2% (22 out of 104) CoTS recorded in this region. Only a single CoTS >50 cm diameter was recorded in the Lizard Island Region in 2021, while the largest CoTS recorded in the Princess Charlotte Bay and Cairns Regions were 49 cm and 39 cm, respectively. The mean size of CoTS recorded in the Cape Grenville Region (43.51 cm ±0.72SE) was substantially higher than recorded in the Princess Charlotte Bay Region (25.00 cm ±2.24SE), the Lizard Island Region (34.89 cm ±1.25SE) and the Cairns Region (24.85 cm ±1.76SE), though there was not a consistent decline in mean size from north to south (Figure 3.3). Rather, small CoTS (10-20cm diameter) accounted for a disproportionate number of CoTS detected in the Princess Charlotte Bay Region (42.86%) and the Cairns Region (35.00%), greatly reducing the mean size of CoTS recorded in these regions.
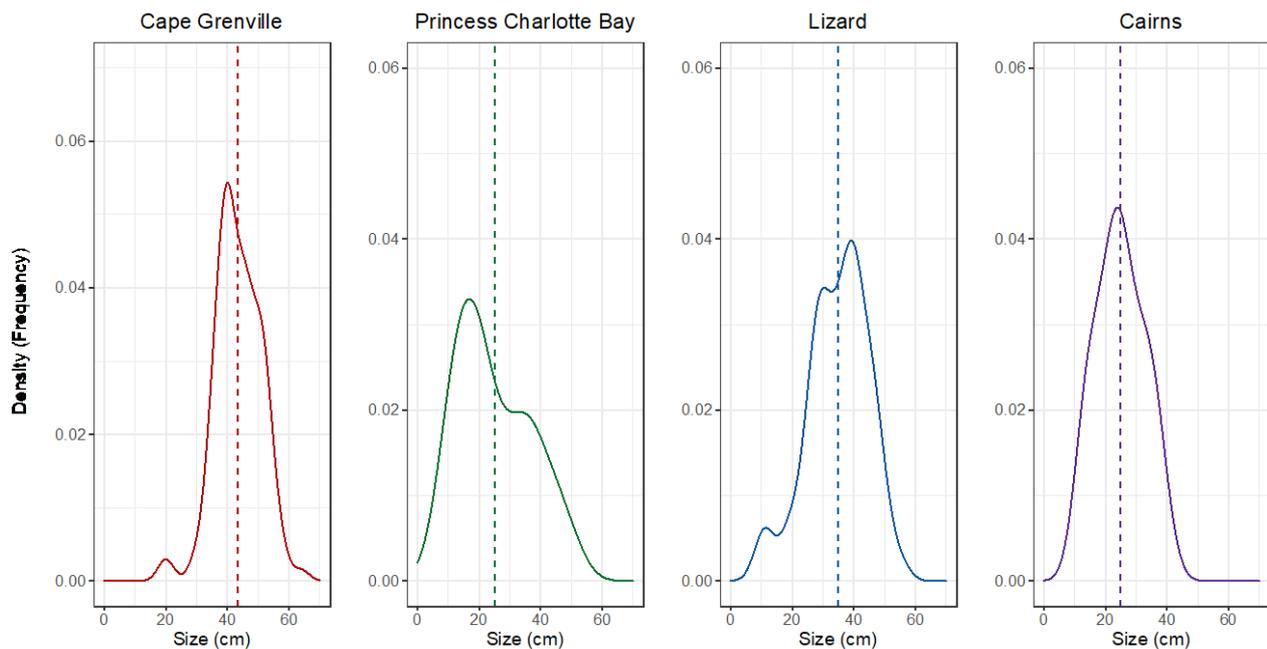
Figure 3.3. Size frequency distributions of CoTS within each of the four distinct regions. Vertical dashed lines show the mean size (in cm) for each region: Cape Grenville Region, mean = 43.51 cm (n = 104); Princess Charlotte Bay Region, mean = 25.00 cm (n = 28); Lizard Island Region, mean = 34.89 cm (n = 62); Cairns Region, mean = 24.85 (n= 20).

3.3 Detectability of CoTS recorded in 2021

During scooter-assisted large area diver-based visual surveys, most CoTS were located only after first sighting conspicuous feeding scars. However, in many cases, 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. Based on these data, the average detectability of CoTS across all surveys where CoTS or feeding scars were recorded (n = 81 surveys) was 46.1% ±3.73SE. Detectability varied greatly among surveys ranging from 0-100% in every region (Figure 3.4). Detectability did however, vary among regions (Figure 3.4): Cape Grenville Region (66.6% ±5.67SE), Princess Charlotte Bay Region (30.7% ±8.11SE), Lizard Island Region (55.2% ±6.39SE) and Cairns Region (30.0% ±6.25SE). Detectability was highest (>50%) in regions (Cape Grenville Region and Lizard Island Region) where CoTS populations were dominated by larger individuals (see Figure 3.3). However, there was no significant or meaningful relationship between detectability and CoTS densities (Figure 3.5).
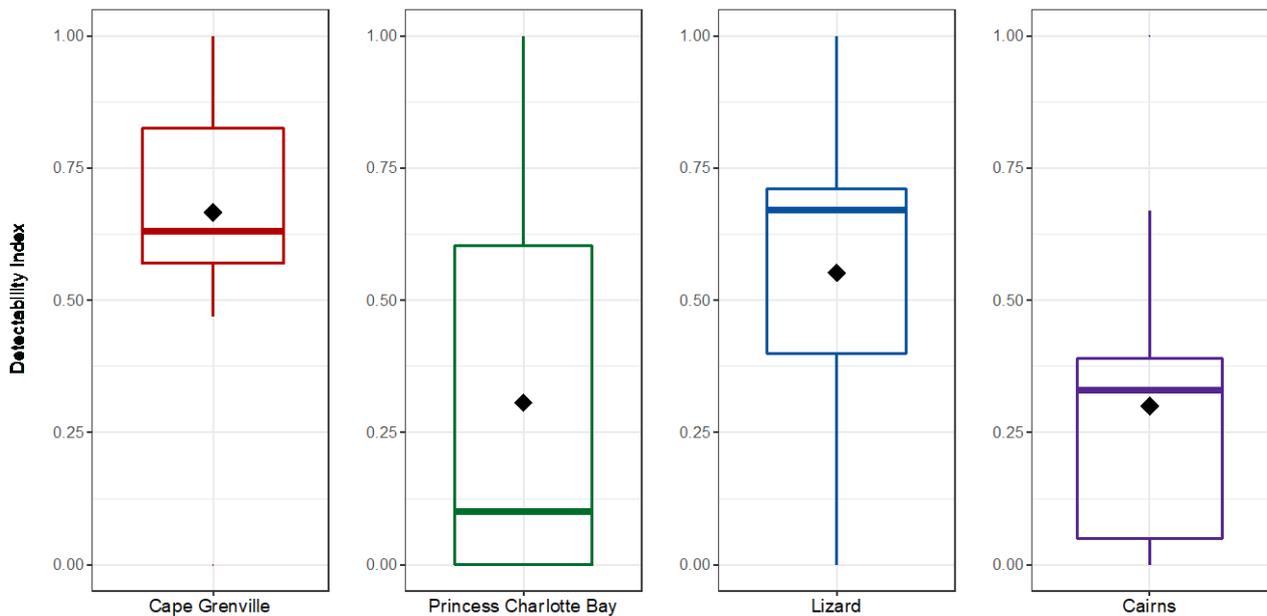
Figure 3.4. Box plots showing regional variation in detectability of CoTS in 2021 from the northern Great Barrier Reef. Each data point represents a single scooter-assisted large area diver-based visual survey. All data is presented as proportion of CoTS actually sighted versus the overall number of CoTS recorded per hectare on each survey (including the number of distinct sets of feeding scars where CoTS were undetected). Black diamonds show the mean detectability recorded per region.
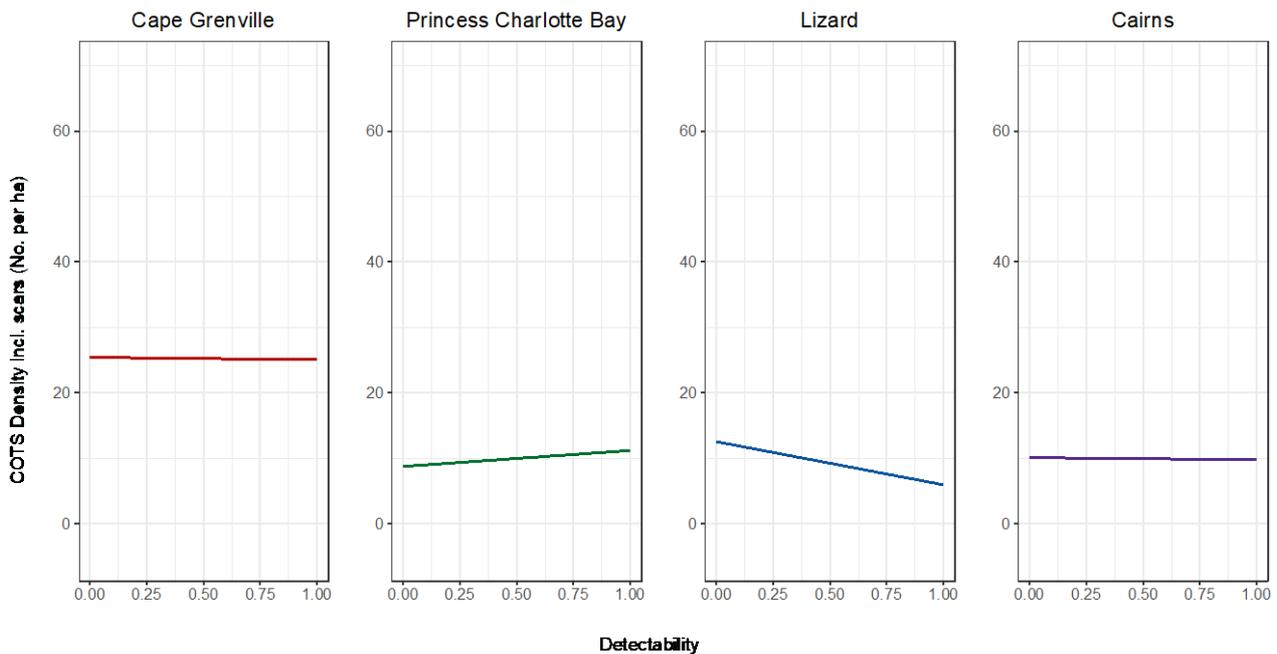
Figure 3.5. Line of best fit and 95% confidence limits for the relationship between detectability and overall density of CoTS recorded on each survey, which was explored separately for each region.

3.4 Temporal changes in the abundance of CoTS

Scooter-assisted large area diver-based visual surveys (as reported above) have now been conducted over three years in the Lizard Island Region. While CoTS densities have remained low (<15 individuals.ha^{-1}) across all four reefs surveyed (MacGillivray Reef, Lizard Island, Eagle

Island and North Direction Island) within this region, recorded densities have increased at Lizard Island and North Direction Island from 2019 to 2021 (Figure 3.6). At Lizard Island, the average density of CoTS increased from 4.38 CoTS.ha^{-1} (±0.81SE) in 2019 (n= 36 surveys) up to 8.83 CoTS.ha^{-1} (±1.72SE) in 2021 (n= 22 surveys). There was a slight decline in the mean density of COTS at Lizard Island from 2019 to 2020, but this was negligible, and the maximum recorded density at any site (mostly found at Clam Gardens) increased consistently across all three years.

Despite comparably limited annual sampling at North Direction Island, there was a marked increase in recorded CoTS densities from 0.65 CoTS.ha^{-1} (±0.65SE) in 2019 (n = 4 surveys) to 4.25 CoTS.ha^{-1} (±0.73SE) in 2020 (n = 4). The number and density of CoTS recorded at North Direction Island also further increased from 2020 to 2021 (Figure 3.6). Densities of CoTS recorded at the other reefs (MacGillivray Reef and Eagle Island) also increased from 2019 to 2020, but then declined to 2021.
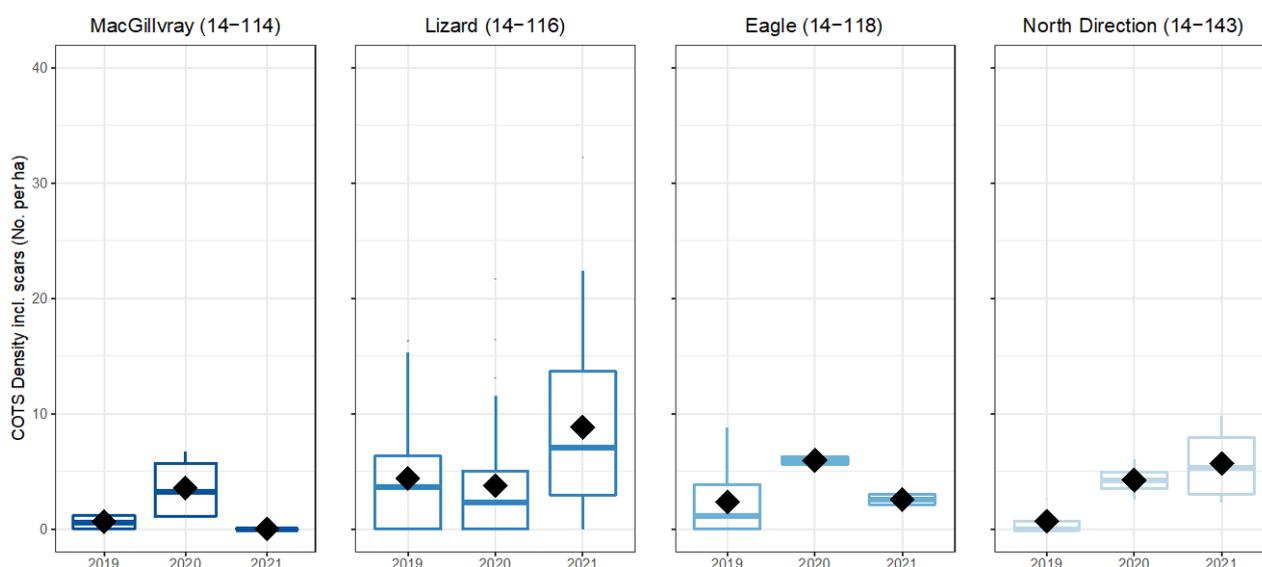
Figure 3.6. Box plots showing interannual variation in CoTS densities at each reef sampled within the Lizard Island Region. Each data point represents a single scooter-assisted large area diver-based visual survey. All data is presented as number of CoTS (including the number of distinct sets of feeding scars where CoTS were undetected) recorded per hectare. Black diamonds show the mean density recorded in each year at each reef.

3.5 eDNA sampling to verify local occurrence of CoTS

Complementary sampling to detect local occurrence and abundance of CoTS, using both diver-based (SALAD surveys) and diver-independent (eDNA) methods have so far (in 2020 and/ or 2021) been conducted at 12 different reefs and 33 sites (Table 3.1). Analysis presented here are at the Reef level.

Processing of samples occurred in three batches, primarily according to the field trips. Batch 1 included the Lizard Island, Cairns and Townsville Region, Batch 2 comprised the Princess Charlotte Bay Region and Batch 3 comprised the Cape Grenville Region. As described in the Methods, false positive correction was applied at the 'trip'/'batch' level. False positive correction was required for Batch 1 (Lizard Island, Cairns and Townsville Region) and Batch 3 (Cape Grenville Region). For the Lizard Island, Cairns and Townsville Region, 1/42 control tests had contamination, whereas for the Cape Grenville Region, 7/96 controls tests had contamination

with each contaminated test containing a single positive droplet in a ddPCR test. The following results have been corrected for false positives.

Reefs in the Cape Grenville area were variable with all eDNA samples collected from McSweeny Reef returning positive (100% positive detection rate), whereas un-named reefs 11-049 and 11-162 had 17% and 28% positive detections respectively. Further south, eDNA results from reefs in the Princess Charlotte Bay Region revealed relatively low positive detection rates at both Davie Reef (6%) and Corbett Reef (14%), which may be indicative of normal background levels (Doyle & Uthicke, 2020). However, positive detection rates were much higher at U/N 13-124 (39%), equivalent to that reported at Lizard Island.

Table 3.1. Positive detection levels for CoTS recorded at individual reefs (% of samples with 95% CI) from eDNA sampling and the corresponding densities of CoTS recorded at each reef using SALAD surveys.

Region	Reef	Positive detection of CoTS as % of samples above LOD (95% CI)	Density of CoTS (no. CoTS.ha^{-1}) recorded from corresponding visual surveys
Cape Grenville	McSweeney	100% (90%-100%)	43.98
	U/N 11-049	17% (8% - 32%)	24.04
	U/N 11-162	28% (16% - 44%)	7.48
Princess Charlotte Bay	Corbett	14% (6% - 29%)	11.32
	U/N 13-124	39% (25% - 55%)	7.20
	Davie	6% (2% - 18%)	2.91
Lizard Island	Lizard Island	33% (26% - 41%)	5.17
Cairns	Thetford	50% (33% - 67%)	15.61
	Moore	63% (46% - 78%)	5.61
	Elford	73% (56% - 86%)	11.57
Townsville	Kelso	90% (74% - 97%)	18.12
	Rib	80% (63% - 91%)	20.47

Extensive eDNA sampling was undertaken at Lizard Island, and at many of the same locations where SALAD surveys have also been conducted (e.g., Big Vicki's Reefs, Mermaid Cove, Clam Gardens and Casuarina Beach). Positive eDNA detections for CoTS have been recorded at all sites around Lizard Island, where the overall detection rate is 33% (Table 3.1). However, detection rates were consistently higher at Clam Gardens, Big Vicki's and Mermaid Cove (40-53%), compared to the Lagoon (7%) and Casuarina Beach (13%). These areas (especially Clam Gardens) also had the highest densities of CoTS, based on visual surveys.

The positive eDNA detection rate of CoTS from reefs in the Cairns Region, ranged from 50% at Thetford Reef to 73% at Elford Reef. However, these detection rates were moderate compared to very high detection rates recorded at Kelso Reef and Rib Reef (Table 3.1).

Environmental DNA assay sensitivity is critical to identifying trace amounts of CoTS eDNA in a small volume of seawater. This presents increased risk to cross contamination of samples, hence

the reason for controls at the field sampling, extraction and amplification stages of the workflow. The presence of contamination in some controls presented herein highlight the importance of thorough equipment cleaning and careful sample handling from collection through to laboratory in order maximise the potential of the eDNA approach.

Positive detection levels recorded at individual reefs were lowest at Davie Reef (6%), where densities recorded using SALAD surveys were also lowest (2.91 CoTS.ha^{-1}). Likewise, the highest detection levels (>80%) were recorded in areas (Townsville Region and McSweeny Reef, Cape Grenville) where the recorded densities of CoTS were highest (Table 3.1). These data show that there is general concordance in recorded densities of CoTS from visual surveys versus diver-independent estimates of the local occurrence of CoTS (% of samples with detection above LOD) based on eDNA sampling (Figure 3.7).
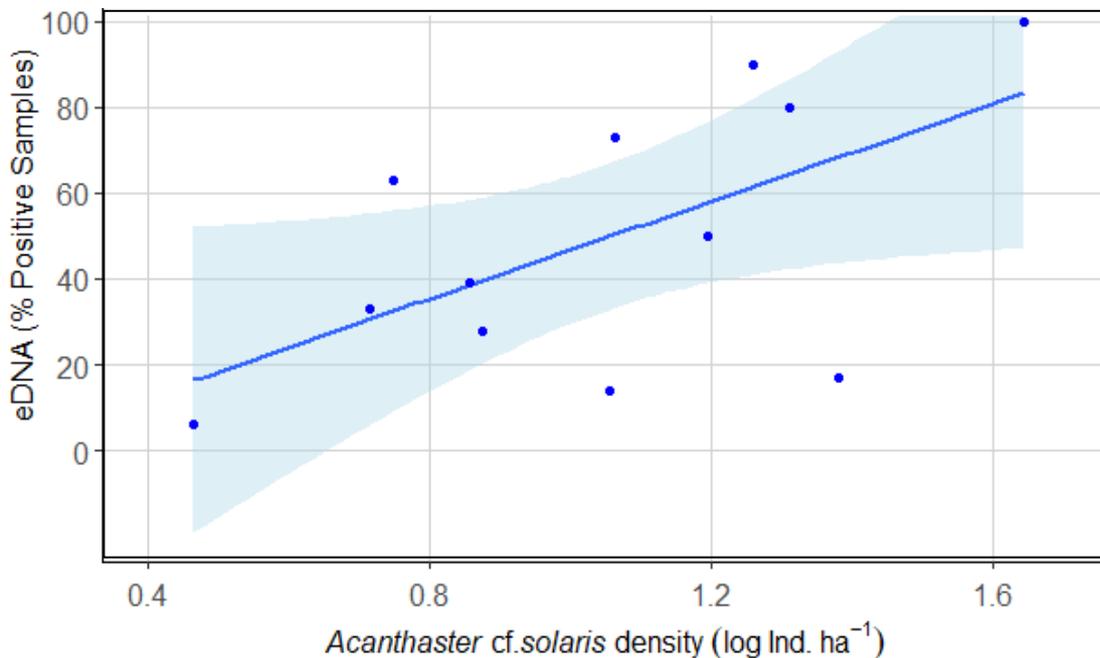

Figure 3.7. Line of best fit and 95% confidence limits for the relationship between reef-level densities of CoTS recorded using scooter-assisted large area diver-based visual surveys, and corresponding levels of positive detections (% of samples with detection above LOD) from eDNA sampling.

4. DISCUSSION

This study demonstrates the utility of scooter-assisted large area diver-based (SALAD) visual surveys for effectively surveying CoTS, even at low densities that typically occur outside of population irruptions (<15 CoTS.ha^{-1}; Moran & De'ath 1992). More specifically, there was general concordance in recorded densities of CoTS from SALAD surveys versus diver-independent estimates of the local occurrence of CoTS, based on eDNA sampling. Moreover, SALAD surveys resolved marked differences in the contemporary (2021) abundance of CoTS among and within regions in the northern GBR, and also demonstrated that there are already are moderate densities of CoTS (>15 CoTS.ha^{-1}) at some reefs in the far northern GBR, well ahead of the anticipated onset of the next major population irruption in 2025-2027 (*sensu* Babcock et al. 2020). Based solely on current survey data, it is not clear that elevated densities of CoTS recorded at reefs off Cape Grenville (e.g., 43.98 CoTS.ha^{-1} ±6.65SE at McSweeney Reef) necessarily represent the origin of renewed population irruptions, nor that the next episode of population irruptions has unequivocally started. Rather, sustained densities of CoTS may be naturally higher at some reefs (Moran & De'ath 1992), and may not necessarily lead to broad-scale population irruptions. These data do however, provide an important baseline for assessing temporal trends in CoTS populations in coming years, thereby providing an unprecedented opportunity to establish when and where population irruptions originate, and better understand the ultimate and proximal cause(s) of population irruptions.

4.1 Potential initiation of renewed population irruptions

Intuitively, the initiation of the next major and distinct episode of population irruptions of CoTS on the GBR should be readily apparent (Babcock et al. 2020), based on sustained increases in CoTS densities at specific reefs within the *initiation box*. However, the onset of previous population irruptions was not clearly evident until densities of CoTS had exceeded threshold densities across several distinct reefs (Sweatman et al. 1998, Pratchett 2005). While there are very large and apparent differences in the abundance of CoTS before versus during population irruptions (Moran & De'ath 1992), considerable uncertainty surrounds the transition period between these two modalities. In many cases, the transition is seemingly very rapid (e.g., Houk & Raubani 2010), which 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). Critically, there are few studies that have undertaken recurrent monitoring using survey methods with capacity to detect cryptic individuals during the initiation of population irruptions, and those studies that have been conducted (e.g., Zann et al. 1990, Pratchett 2005) were very restricted in spatial scale.

This study provides an important platform and baseline data for potentially assessing interannual variation in the abundance of CoTS in coming years, which will provide much more certainty regarding the potential initiation of renewed population irruptions of CoTS on the GBR. Notably, however, there is strong evidence that SALAD surveys need to be conducted not only in within the area of the putative initiation box, but also at reefs well north of this area (especially in the Cape Grenville Region). It may be premature to suggest that the current designation of the *initiation box* (Figure 1.1) is incorrect, but research is certainly warranted at reefs well outside of this area.

The designation of a distinct *initiation box* for population irruptions of CoTS on the GBR (Dight et al. 1990, James & Scandol 1992, Fabricius et al. 2010) has unequivocally focused research attention on reefs within this area (e.g., Hock et al. 2014, Wooldridge & Brodie 2015, MacNeil et al. 2017). This is not only because elevated densities of CoTS were first observed at reefs in the Cairns Region or Lizard Island Regions during each of the four documented population irruptions (Pearson & Endean 1969, Reichelt et al. 1990, Pratchett 2005), but because reefs in this area are characterised by strong local hydrodynamic connections (James & Scandol 1992, Hock et al. 2014, Wooldridge & Brodie 2015), which may facilitate high levels of larval retention and progressive increases in CoTS densities over several successive cohorts. Sustained increases in CoTS densities at these reefs (Pratchett 2005) do not however, necessarily result from the accumulation of larvae of local progeny. Rather, these reefs may concentrate larvae spawned by established populations of CoTS on a broad range of upstream reefs.

While elevated densities of CoTS are already apparent in the northern GBR (Cape Grenville Region), there is also evidence of recent increases in CoTS densities at Lizard Island and North Direction Island (Figure 3.6), where CoTS densities have more than doubled in the two years since 2019. Previously, population irruptions of CoTS at Lizard Island resulted from highly protracted increases in CoTS densities (Pratchett 2005), such that these data may signal the early onset of a population irruption. At the current rate of population growth (recorded from 2019-2021), it is likely that CoTS densities will exceed notional thresholds of population irruptions (15 CoTS.ha^{-1}) at Lizard Island within the next 2 years. However, extensive surveys undertaken at Lizard island did indicate declines in CoTS densities from 2019 to 2020 (Figure 3.6), which may be due to sustained culling during this period. If so, it is clear even greater culling effort may be required to suppress the proliferation of CoTS at this location. Moreover, if CoTS settling at Lizard Island are originating from established populations of relatively large CoTS on reefs in the far northern GBR, suppressing future population irruptions may require broad-scale culling at a range of reefs and well north of the currently prescribed *initiation box.*

4.2 Recurrent monitoring and critical knowledge gaps

This study has provided important insights into the contemporary status of CoTS populations in the northern GBR, which reaffirms observations of increasing CoTS densities as well as already high densities of CoTS at some reefs (www.aims.gov.au/reef-monitoring/cape-grenville-sector-2021), heightening concerns regarding the impending onset of renewed population irruptions (Babcock et al. 2020). However, given that there has been very limited previous and recurrent sampling of low-density CoTS populations the importance and relevance of these data are very uncertain. It is very important, therefore, that the surveys described in this study are extended and repeated. At a minimum, we are committed to recurrent annual surveys over the next three years (2022-2024) with support from CCIP (Project CCIP-P-04), to test for interannual changes in distribution, abundance and size-structure of CoTS populations at previously surveyed reefs in each of the four distinct regions (Cape Grenville, Princess Charlotte Bay, Lizard Island and Cairns).

Recurrent monitoring of CoTS populations in the northern GBR is critical for providing information to improve the ecological underpinning for the effective management of population irruptions, which remain one of the major causes of coral loss and reef degradation on the GBR (Mellin et al. 2019). Aside from potentially informing pre-emptive culling to supress apparent increases in CoTS densities and thereby prevent (or contain) renewed population irruptions, early detection and effective monitoring of population irruptions is critical for resolving persistent controversies regarding the cause(s) of population irruptions. 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 Cape Grenville Region, and also further explore potential linkages between established populations of large CoTS in the far northern GBR and apparent increases in CoTS densities at Lizard Island. This will require greatly increased survey effort in the far northern GBR, but also timely deployment of drag current meters to validate and improve hydrodynamic models for the far northern GBR, following Wolanski and Lambrechts (2020). Some hydrodynamic models (Hock et al. 2014) have highlighted the potential importance of reefs in the far northern GBR, though there has been extremely limited research in this region, especially compared to the area between Lizard Island and Cairns.

4.3 Conclusions

Established methods for surveying and monitoring CoTS populations on the GBR (especially manta-tow surveys) have demonstrated utility for providing timely information (and at scale) on the spatiotemporal occurrence of population irruptions (Moran et al. 1998, Vanhatalo et al. 2017). These data are also critical to the strategic planning and effectiveness of manual CoTS control across the GBR (Westcott et al. 2020). However, new and more ambitious management goals (such as the suppression of CoTS densities even before the initiation of population irruptions) will require more refined and resolved survey information. Most notably, new methods are needed to increase efficiency and effectiveness of sampling low-density CoTS populations, as well as for sampling in areas that cannot be readily assessed using established (largely diver-based) methods.

This study has demonstrated the utility of two different and highly complementary methods for assessing the occurrence and abundance of CoTS across a broad range of densities.

REFERENCES

Babcock RC, Dambacher JM, Morello EB, Plagányi ÉE, Hayes KR, Sweatman HP, Pratchett MS (2016) Assessing different causes of Crown-of-Thorns Starfish outbreaks and appropriate responses for management on the Great Barrier Reef. *PLoS ONE* 11: e0169048.

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.

Baumann JH, Zhao LZ, Stier AC, Bruno JF (2021) Remoteness does not enhance coral reef resilience. Global Change Biology 28(2):417-428.

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.

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

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.

Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2(8):e711.

Chesher RH (1969) Destruction of Pacific corals by the sea star *Acanthaster planci. Science* 165(3890):280-283.

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27–year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences, USA* 109(44):17995-17999.

Dight IJ, James MK, Bode L (1990) Modelling the larval dispersal of *Acanthaster planci. Coral Reefs* (3):125-134.

Doyle J, Uthicke S (2020) 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.

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.

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

Ficetola GF, Miaud C, Pompanon F, Taberlet P (2008) Species detection using environmental DNA from water samples. *Biology Letters* (4):423-425.

Ganter R (1987) Oral history of human use and experience of crown of thorns starfish on the Great Barrier Reef. Report to the Great Barrer Reef Marine Park Authority, 31pp.

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.

Haszprunar G, Vogler C, Wörheide G (2017) Persistent gaps of knowledge for naming and distinguishing multiple species of crown-of-thorns-seastar in the *Acanthaster planci* species complex. *Diversity* 9(2):22.

Hobbs JA, Salmond JK (2008) Cohabitation of Indian and Pacific ocean species at Christmas and Cocos (Keeling) islands. *Coral Reefs* 27(4):933.

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.

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.

Hunter ME, Meigs-Friend G, Ferrante JA, Kamla AT, Dorazio RM, Diagne LK, Luna F, Lanyon JM, Reid JP (2018) Surveys of environmental DNA (eDNA): a new approach to estimate occurrence in vulnerable manatee populations. *Endangered Species Research* 35:101-111.

James MK, Scandol JP (1992) Larval dispersal simulations: correlation with the crown-of-thorns starfish outbreaks database. *Marine and Freshwater Research* 43(3):569-581.

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.

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.

Kenchington RA (1977) Growth and recruitment of *Acanthaster planci* on the Great Barrier Reef. *Biological Conservation* 11:103-118.

Kenchington RA, Pearson R (1982) 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.

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.

MacNeil MA, Chong-Seng KM, Pratchett DJ, Thompson CA, Messmer V, Pratchett MS (2017) Age and growth of an outbreaking *Acanthaster* cf. *solaris* population within the Great Barrier Reef. *Diversity* 9(1):18.

Majaneva M, Diserud OH, Eagle SH, Boström E, Hajibabaei M, Ekrem T (2018) Environmental DNA filtration techniques affect recovered biodiversity. *Scientific Reports* 8(1):14682.

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.

Mellin C, Peterson EE, Puotinen M, Schaffelke B (2020) Representation and complementarity of the long-term coral monitoring on the Great Barrier Reef. *Ecological Applications* 30(6):e02122.

Moore RJ (1978) Is *Acanthaster planci* an r-strategist?. *Nature* 271(5640):56-57.

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

Moran PJ, Bradbury RH, Reichelt RE (1988) Distribution of recent outbreaks of the crown-of-thorns starfish (*Acanthaster planci*) along the Great Barrier Reef: 1985–1986. *Coral Reefs* 7(3):125-137.

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(3):509-515.

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.

Pearson RG (1981) Recovery and recolonization of coral reefs. *Marine Ecology Progress Series* 31:105-122.

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.

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.

Pratchett MS. Dynamics of an outbreak population of *Acanthaster planci* at Lizard Island, northern Great Barrier Reef (1995–1999). Coral Reefs 24(3):453-462.

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.

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.

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 (2021) 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.

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.

Sweatman H (2008) No-take reserves protect coral reefs from predatory starfish. *Current Biology* 18(14):R598-599.

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.

Sweatman H, Delean S, Syms C (2011) Assessing loss of coral cover on Australia's Great Barrier Reef over two decades, with implications for longer-term trends. Coral Reefs 30(2):521-531.

Thomsen PF, Willerslev E (2015) Environmental DNA–An emerging tool in conservation for monitoring past and present biodiversity. *Biological Conservation* 183:4-18.

Thomsen PF, Kielgast J, Iversen LL, Møller PR, Rasmussen M, Willerslev E (2012) Detection of a diverse marine fish fauna using environmental DNA from seawater samples. *PLoS ONE* 7(8):e41732.

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.

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.

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* 37:1229-1239.

Uthicke S, Fisher EE, Patel F, Diaz-Guijarro B, Doyle JR, Messmer V, Pratchett MS (2019) Spawning time of *Acanthaster cf. solaris* on the Great Barrier Reef inferred using qPCR quantification of embryos and larvae: do they know it's Christmas? *Marine Biology* 166: 133

Vanhatalo J, Hosack GR, Sweatman H (2017) Spatio-temporal modelling of crown-of-thorns starfish outbreaks on the Great Barrier Reef to inform control strategies. *Journal of Applied Ecology* 54:188-197.

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

Weber JN, Woodhed PMJ (1970) Ecological studies of the coral predator *Acanthaster planci* in the South Pacific. *Marine Biology* 6(1):12-17.

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.

Wolanski E, Lambrechts J (2020) The net water circulation in the far Northern Great Barrier Reef. *Estuarine, Coastal and Shelf Science* 235:106569.

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.

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.

Morgan S. Pratchett (morgan.pratchett@jcu.edu.au)
ARC Centre of Excellence for Coral Reef Studies,
James Cook University, Townsville, Queensland 4811

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