Coral Reefs
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RESEARCH

Detectability of Pacific crown-of-thorns starfish (*Acanthaster* cf. *solaris*) using scooter-assisted large area diver-based (SALAD) surveys in the Northern Great Barrier Reef, Australia

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Abstract Limited detectability of crown-of-thorns starfish (CoTS) undermines the capacity to survey and manage population irruptions, though few studies have considered the factors that influence detectability. This study explores spatiotemporal variation in detectability of CoTS during emerging population irruptions in four regions of the Northern Great Barrier Reef (GBR), by comparing recorded densities based on the number of CoTS sighted to inferred densities that account for distinct sets of feeding scars, which are presumed to indicate the localised occurrence of starfish that cannot be detected. Mean detectability was estimated to be 50.51% (±1.59SE) across all scooter-assisted large area diver-based (SALAD) surveys where CoTS or feeding scars were recorded ($n = 405$ surveys), ranging from 29.59% (±4.22SE) up to 59.46% (±2.69SE) among regions. Regional differences in detectability correspond with differences in the size of CoTS, whereby larger CoTS tended to be more exposed, and marked differences in the proportion of CoTS recorded feeding. The average exposure increased with size of CoTS, with an asymptote at approximately 60% for CoTS > 500 mm diameter. Proportional exposure of individual CoTS was also strongly affected by feeding, whereby CoTS that were feeding during the day were generally completely exposed. This study reaffirms that limited detectability of CoTS needs to be taken into account when estimating absolute densities using different survey methods. These data also highlight significant limitations of survey methods (e.g. manta tow and towed camera) that rely on visual detection from above to estimate CoTS densities.

Keywords Coral reefs · Disturbance · Management · Surveillance · Sampling

Introduction

Crown-of-thorns starfish (CoTS; *Acanthaster* spp.) represent one of the major causes of coral mortality, especially in locations with persistent or recurrent population irruptions (e.g. Southern Japan, Yamaguchi 1986; Australia's Great

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Barrier Reef, De'ath et al. 2012; Moorea, Kayal et al. 2012). CoTS cause extensive coral mortality by feeding directly on live corals, and their feeding capacity scales with body size (e.g. Keesing and Lucas 1992), such that combined feeding activities of high densities of large starfish can 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 around Moorea between 2005 and 2010 (Kayal et al. 2012). Accordingly, there are significant and widespread efforts to manage population irruptions of CoTS, by culling or removing adult individuals (Bos et al. 2013; Matthews et al. 2024).

Population irruptions of CoTS (also referred to as outbreaks; Weber and Woodhead 1970) have been reported on reefs throughout the Indo west-Pacific (Foo et al. 2024; Uthicke et al. 2024a), including recent outbreaks of *Acanthaster planci* and/or *Acanthaster mauritiensis* in the Gulf of Oman (Seveso et al. 2024) and widespread reports of population irruptions of *Acanthaster* cf. *solaris* throughout the western and central Pacific (e.g. Kayal et al. 2012; Timmers et al. 2012; Baird et al. 2013). 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 relative to specific threshold densities (Pratchett et al. 2014). Part of the issue in defining and distinguishing population irruptions relates to inherent challenges in quantifying densities of CoTS, especially at relatively low or moderate densities (Chandler et al. 2023). Critically, CoTS may be highly cryptic, especially when small, at low densities, and during daylight hours, making it very difficult to establish "normal" or baseline densities (Weber and Woodhead, 1970; Moran 1986; Fernandes et al. 1990; Kayal et al. 2017). By contrast, CoTS are very conspicuous during population irruptions, but even then, it is difficult to establish absolute densities (Kayal et al. 2017). In particular, smaller individuals may evade detection (MacNeil et al. 2016), leading to misapprehensions about population structure.

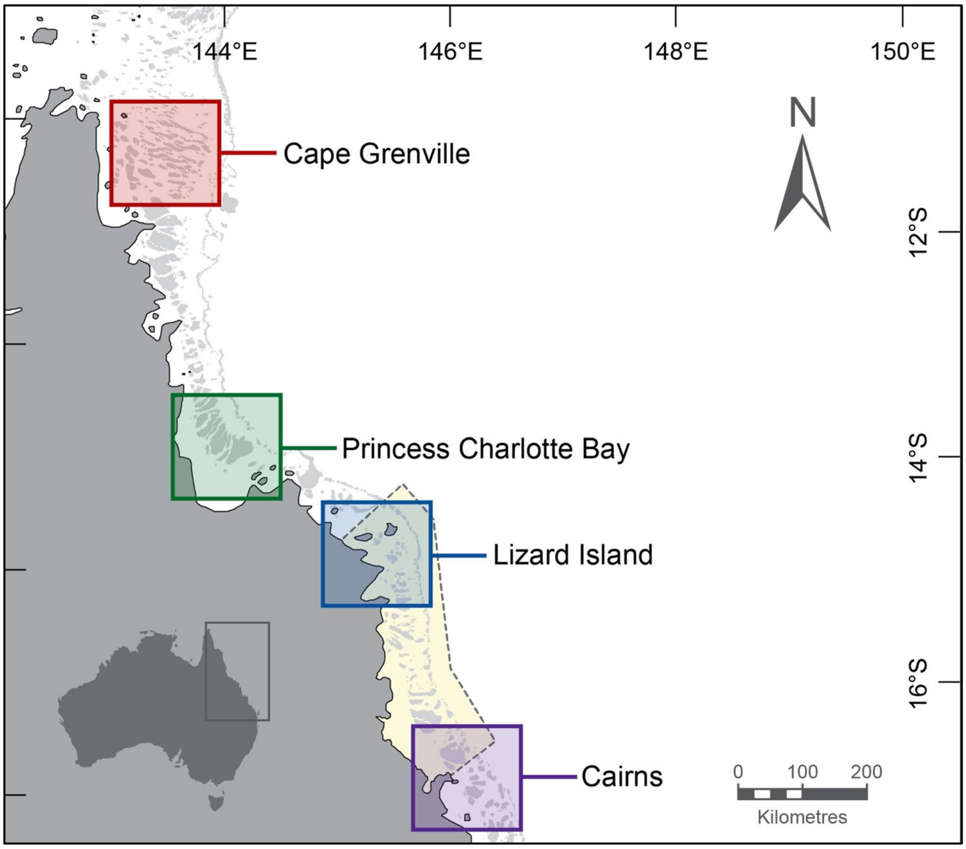
Detectability is the *Achilles heel* of effective monitoring and management for pest organisms (e.g. Hayes et al. 2005; Britton et al. 2011), though detectability of CoTS has rarely been considered, let alone quantified (Saponari et al. 2018, Dumas et al. 2020, Matthews et al. 2024; but see Fernandes et al. 1990, MacNeil et al. 2016, Kayal et al. 2017, Pratchett and Caballes 2025). Fernandes et al. (1990) estimated that < 5% of CoTS are likely to be detected during manta tow surveys, emphasising that these methods, while appropriate for broad-scale assessments of the incidence of population irruptions, have limited utility for estimating absolute densities. Conversely, detectability of CoTS during intensive surveys along 50 m belt transects has been estimated to be 73–82% (MacNeil et al. 2016; Kayal et al. 2017; Pratchett and Caballes 2025). These estimates are based on recurrent sampling along fixed transects, comparing initial estimates obtained during the day versus the number of additional CoTS recorded during subsequent surveys, including sampling at night. High levels of detectability were attributed to the intensive search effort concentrated in a relatively finite area (MacNeil et al. 2016). Detectability is also expected to vary with coral cover and habitat structure, and corresponding changes in behavioural modality of CoTS (Moran 1986; Fernandes et al. 1990). De'ath and Moran (1998) showed that smaller CoTS (< 300 mm diameter) tend to be more cryptic and feed predominantly at night, whereas larger individuals have less distinct diurnal patterns of feeding. Patterns of feeding (and movement) are further dictated by the local availability of preferred coral prey (Ling et al. 2020), with starfish exhibiting strong fidelity to specific resting locations when food is abundant.

The purpose of this study was to assess spatiotemporal variation in detectability and exposure of CoTS during emerging population irruptions in the Northern Great Barrier Reef (GBR). There have been four separate population irruptions recorded on the GBR since 1960s (Pratchett et al. 2017), and renewed population irruptions were expected to arise in 2025–2027 (Babcock et al. 2020), based on the periodicity of former irruptions. Accordingly, highly resolved sampling at Lizard Island has detected increasing densities of CoTS since 2021 (Chandler et al. 2023; Uthicke et al. 2024b). The purpose of the current study was not to assess CoTS densities, or variation therein, but explicitly consider detectability and exposure of CoTS. Detectability was estimated based on the number of CoTS that were sighted relative to the inferred number of CoTS present along extensive transect areas, where the latter was based on the occurrence of conspicuous feeding scars. Exposure, meanwhile, was the extent to which individual starfish were concealed within the reef matrix versus visible from directly above, following Burn et al. (2020). Detectability is expected to increase with increasing exposure, but these two distinct metrics were measured at different scales and provide different insights into the role of extrinsic (e.g. coral cover and habitat complexity) versus intrinsic factors (individual size and behaviour) that affect the likelihood of sighting individual CoTS using different survey methods.

Methods

Annual sampling (mostly in summer; December to February) was conducted over 5 years (2021–2025) in each of four distinct regions across the Northern (Cairns region and Lizard Island region) and Far Northern sectors (Princess Charlotte Bay region and Cape Grenville region) of the

Fig. 1 Map of the Northern Great Barrier Reef, showing the putative initiation box (shown in yellow), where population irruptions of western Pacific CoTS (*Acanthaster* cf. *solaris*) are reported to originate. Labels indicate four distinct regions where sampling was undertaken to test for variation in detectability and exposure of CoTS using SALAD surveys in 2021–2025



GBR (Fig. 1). Sampling in the Cairns versus Lizard Island regions was undertaken to assess the relative timing of the initiation of impending population irruptions in the northern versus southern extent of the putative initiation box (Fig. 1). Sampling was also undertaken in the two distinct regions located well-north of this area (Princess Charlotte Bay and Cape Grenville regions), as previous sampling has detected elevated densities of CoTS in the far Northern GBR ahead of the reported initiation of population irruptions in the Lizard Island region (Vanhatalo et al. 2017).

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

During SALAD surveys, most CoTS were located only after first sighting conspicuous 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 10 m from the most recent feeding scar) to locate the starfish. For every CoTS detected, divers recorded i) the size of the starfish (maximum diameter to the nearest 5 mm), ii) time of day, iii) depth, iv) the proportion of the starfish that was visible from directly above as a measure of exposure, and v) whether the CoTS was actively feeding. In instances where CoTS could not be found (and were presumably hidden within the reef matrix), each distinct cluster of scars was used to infer the local presence of an individual CoTS, assuming multiple feeding scars within the same general vicinity were considered to be caused by a single CoTS. Counts of distinct sets of feeding scars were summed together with the number of CoTS recorded and divided by search area to gain overall inferred CoTS densities, following Chandler et al. (2023). Detectability was therefore estimated based on the number of CoTS that were sighted (recorded density) divided by the inferred density for each SALAD survey.

Spatiotemporal variation in coral cover and habitat structure was assessed using 50 m point-intercept transects (PIT).

Two replicate PITs were surveyed within the area encompassed by each SALAD survey, generally at the start and end of each survey. The specific organisms or type of substrate underlying each of 100 uniformly spaced points (50 cm apart) were recorded along each PIT, following Pratchett et al. (2009). Topographic complexity was visually estimated (on a scale from 0–5) at the start of each PIT looking down the intended track of the transect line, following Wilson et al. (2007). Hard coral cover (expressed as a proportion of all sampling points, regardless of underlying substrate) and visual assessments of complexity were averaged across the two replicate transects for each SALAD survey. The limited scale of these coral and habitat surveys poorly reflects and represents the spatial extent of corresponding SALAD surveys, but was mainly intended to assess regional differences in coral cover and habitat structure.

Detectability of CoTS was analysed using generalised linear mixed models (GLMM) with binomial distributions (with logit link functions), given that the range of values was 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). Data were pooled across all years, as interannual changes in detectability are likely to be affected by changes in the size of CoTS and corresponding changes in their behaviour. It was expected that detectability may increase with the size of CoTS (sensu Houk and Raubani 2010). However, it was not possible to explore specific effects of starfish size in this model. We did record the size of all starfish detected, but given the limited densities and detectability, this was not considered sufficient to effectively represent the size structure of CoTS populations for each SALAD survey. To explore variation in exposure of individual CoTS (also referred to as emergence; Keesing 1995), we recorded the approximate proportion of each individual starfish that was visible from directly above. This value was generally either 0, where starfish was fully concealed within the reef matrix, or 1, where the entire starfish was visible from directly above. Proportional exposure was also modelled using a GLMM with a Tweedie distribution and corresponding log link function, which effectively accounted for non-linear effects. Unlike detectability (which was quantified at the scale of SALAD surveys), exposure was recorded for each individual starfish ($n = 1{,}214$).

Alternative models were constructed with *glmmTMB* (McGillycuddy et al. 2025), in R 4.4.2 (R Core Team 2024). All models include reef as a random effect. Models of increasing complexity were compared using Akaike Information Criterion corrected for small sample sizes (AICc) to the best fitting combination of categorical and continuous predictors (Supplementary Table), using the MuMIn package (Bartoń 2025). Each model was validated, and goodness of fit was checked visually and statistically, confirming model convergence, dispersion, and limited collinearity using the *performance* package (Lüdecke et al. 2021). The best model to account for detectability of CoTS measured on each SALAD survey included region and habitat complexity (Supplementary Table 1B), with limited additional information provided when considering zone, time of day, or local coral cover. The best model to account for proportional exposure of individual CoTS included feeding and interaction between size and region (Supplementary Table 2B), with limited additional information provided when considering depth and/or time of day.

Results

A total of 481 SALAD surveys were conducted across 20 reefs, within the four study regions, from 2021 until 2025, with a combined survey area of 205.90 hectares (Table 1).

Table 1 Regional differences in sampling intensity and corresponding densities of crown-of-thorns starfish (CoTS), which were established using scooter-assisted large area diver-based (SALAD) surveys in the Northern (Cairns region and Lizard Island region) and Far Northern sectors (Princess Charlotte Bay region and Cape Grenville region) of the GBR. Also, shown are regional differences in coral cover and habitat complexity, which were recorded along replicate 50 m long transects ($n = 2$ transects), within the area encompassed by each SALAD survey

	Cairns region	Lizard Island region	Princess Charlotte Bay region	Cape Grenville region	Total
Number of SALAD surveys	94	211	79	97	481
Total area surveyed (hectares)	46.44	8067	38.41	40.37	205.90
Number of CoTS detected	53	679	118	364	1214
CoTS feeding (%)	3.77	12.55	25.42	70.56	25.42
Recorded CoTS density (CoTS.ha^{-1})	1.22 (±0.21 SE)	11.94 (±1.00 SE)	4.21 (±0.84 SE)	10.01 (±0.84 SE)	8.19 (±0.53 SE)
Inferred CoTS density (CoTS.ha^{-1})	4.11 (±0.49 SE)	20.28 (±1.40 SE)	8.74 (±1.42 SE)	17.10 (±1.30 SE)	14.43 (±0.77 SE)
Coral cover (%)	27.99 (±1.30 SE)	47.73 (±1.80 SE)	33.67 (±1.74 SE)	27.60 (±1.11 SE)	33.85 (±0.85 SE
Habitat complexity	2.49 (±0.07 SE)	2.41 (±0.10 SE)	2.42 (±0.09 SE)	2.16 (±0.08 SE)	2.37 (±0.04 SE)

A total of 1,214 CoTS were recorded across all SALAD surveys, as well as a further 1,047 distinct sets of feeding scars where the relevant CoTS was not detected. The overall detectability of CoTS (based on the ratio of recorded densities to inferred densities) was 53.69%. However, average detectability across all SALAD surveys where there was at least 1 CoTS or feeding scar ($n = 405$) was 50.52% (± 1.59 SE). Detectability varied greatly among SALAD surveys ranging from 0 to 100% in every region (Fig. 2a) but was generally highest in the Cape Grenville region (averaging 59.47% ± 2.69 SE) and Lizard Island region (55.07% ± 2.16 SE). Detectability was comparatively much lower in the Princess Charlotte Bay region (42.51% ± 4.67 SE) and Cairns region (29.59% ± 4.22 SE) (Fig. 2a).

Regional differences in detectability of CoTS were significant (Table 1), with detectability recorded in Cairns being significantly lower than at all other regions. While habitat complexity was included in the best model (Table 1), and detectability decreased with increasing habitat complexity, from 63% when complexity was < 1.0 down to < 40% where complexity was > 4.0, this was not significant (Table 1). While the statistical model for detectability did not consider the size of starfish, regional differences in mean detectability (Fig. 2a) corresponded closely with regional differences in the mean size (diameter) of CoTS (Fig. 2b). The mean size of CoTS was highest in the Cape Grenville region (401.64 mm ± 3.85 SE) and Lizard Island region (399.59 mm ± 3.55 SE) where detectability was also highest. By comparison, the mean size of CoTS was much lower in the Princess Charlotte Bay (258.66 mm ± 8.98 SE) and Cairns regions (290.38 mm ± 12.11 SE), where detectability was lowest (Fig. 2). There were also marked regional differences in the proportion of CoTS that were recorded feeding, whereby the majority of CoTS detected in the Cape Grenville region were recorded feeding (254 out of 360 individuals), whereas the < 50% of CoTS were recorded feeding in other regions (Table 1).

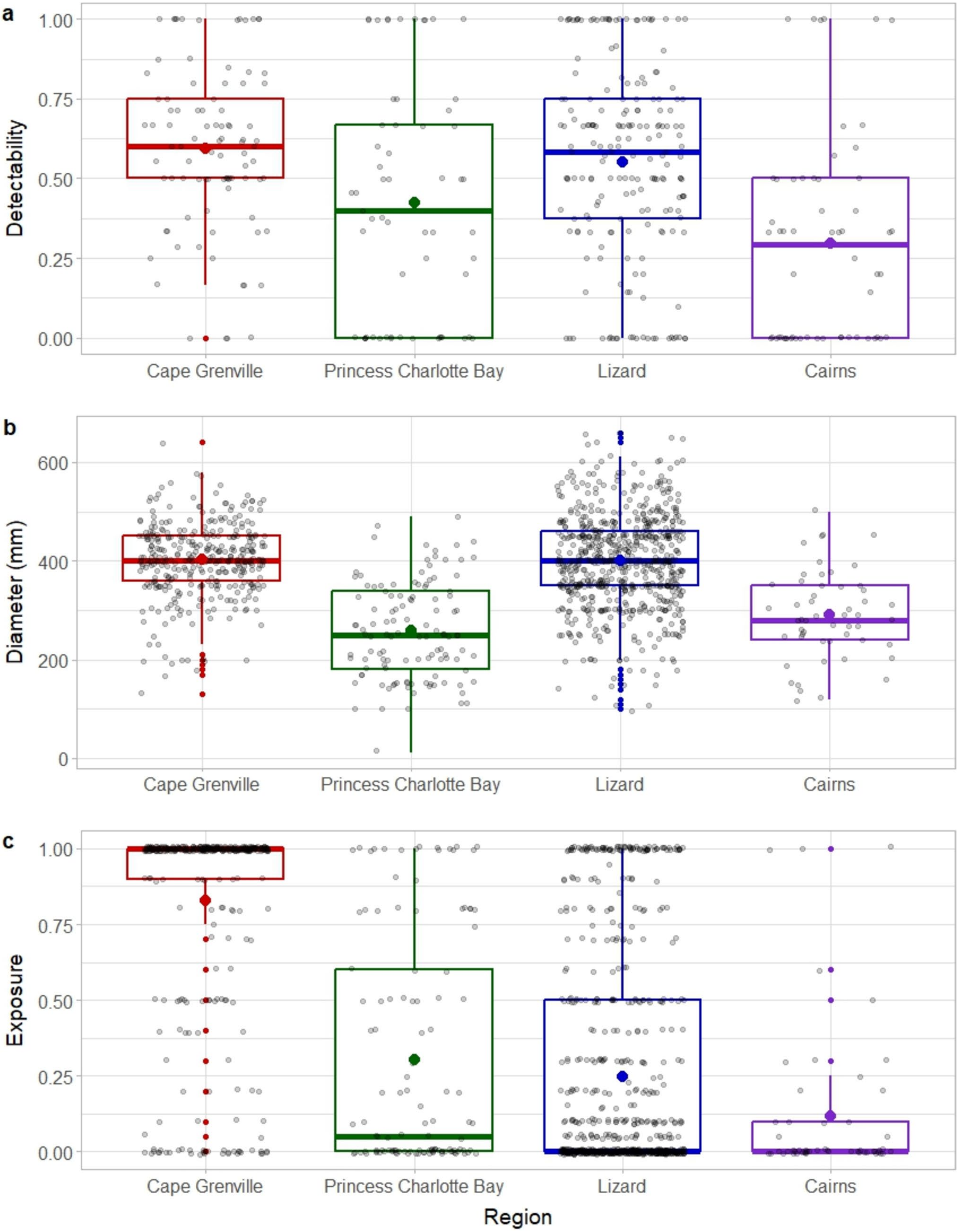
The average level of exposure recorded across all CoTS was 41.80% (± 1.25 SE), though most starfish were either completely concealed (exposure = 0.0: 39.95%) or out in the open and completely visible from above (exposure = 1.0: 29.90%). The average level of exposure was much higher for CoTS recorded in the Cape Grenville region (82.90% ± 1.76 SE), compared to Princess Charlotte Bay (30.38% ± 3.50 SE) and Lizard Island (24.71% ± 1.38 SE) (Fig. 2c). The lowest levels of exposure were recorded in the Cairns region (11.60% ± 3.49 SE). Moreover, most CoTS recorded in Cape Grenville were completely exposed (73.33%), whereas most CoTS recorded in Lizard Island and Cairns regions were completely concealed (52.67% and 67.92%, respectively). Those starfish that were completely exposed were mostly found feeding (71.60%), whereas starfish that were completely concealed were rarely recorded feeding (4.91%). Overall, 25.42% of starfish recorded were found feeding, and mean exposure recorded for feeding starfish was 82.62% (± 1.66 SE) (Fig. 3). For starfish that were detected but not feeding, mean exposure was 23.91% (± 1.24 SE).

Exposure of CoTS varied significantly with feeding, and there was also significant interaction between size and region (Table S2). Proportional exposure increased with increasing size of CoTS in the Cape Grenville, Princess Charlotte Bay, and Lizard regions, but this relationship was not evident in the Cairns region (Fig. 4), where there was a negative relationship between size and exposure. While exposure increased with size in all other regions, the level of exposure recorded for a given size of CoTS was higher in the Far Northern regions (Cape Grenville and Princess Charlotte Bay) than it was at Lizard Island (Fig. 4). This corresponds with regional differences in the proportion of CoTS that were recorded feeding (Table 1).

Discussion

Detectability of marine organisms is typically measured as the portion of individuals, infestations or impacts that are recorded using a given survey or surveillance method (e.g. Britton et al. 2011; Katsanevakis et al. 2012; MacNeil et al. 2016). This assumes that true abundance or absolute densities are known, which is generally not possible for studies conducted in natural environments. Accordingly, detectability is often assessed using experimental studies (Britton et al. 2011) or simulations (e.g. Monroe et al. 2019). In natural environments meanwhile, sampling is designed to maximise detectability and in turn, detectability is assumed to be very high (if not perfect), or at least constant (Katsanevakis et al. 2012; Monroe et al. 2019). There is, however, increasing evidence of imperfect detectability, especially in marine environments (Katsanevakis et al. 2012). Methods required to explicitly quantify and account for detectability (e.g. mark-recapture surveys) typically require repeated sampling in fixed areas (e.g. MacNeil et al. 2016), which greatly constrains the total survey area (e.g. Kayal et al. 2012). In this study, evidence of recent feeding activity was used to provide an independent indicator of the local presence of CoTS, providing the opportunity to quantify detectability without repeated sampling. Inherent assumptions of this approach will affect estimates of detectability, and corresponding inferences regarding absolute densities (Chandler et al. 2023). However, this approach provides estimates of detectability at unprecedented scales, and corresponding insights into the factors that drive variation in detectability from individual behaviour to habitat structure.

SALAD surveys provide divers with autonomy to stop and search for CoTS as needed, especially within the vicinity of recent feeding scars. Even so, the detectability of


a
Detectability
1.00
0.75
0.50
0.25
0.00
Cape Grenville
Princess Charlotte Bay
Lizard
Cairns
b
Diameter (mm)
600
400
200
0
Cape Grenville
Princess Charlotte Bay
Lizard
Cairns
c
Exposure
1.00
0.75
0.50
0.25
0.00
Cape Grenville
Princess Charlotte Bay
Lizard
Cairns
Region

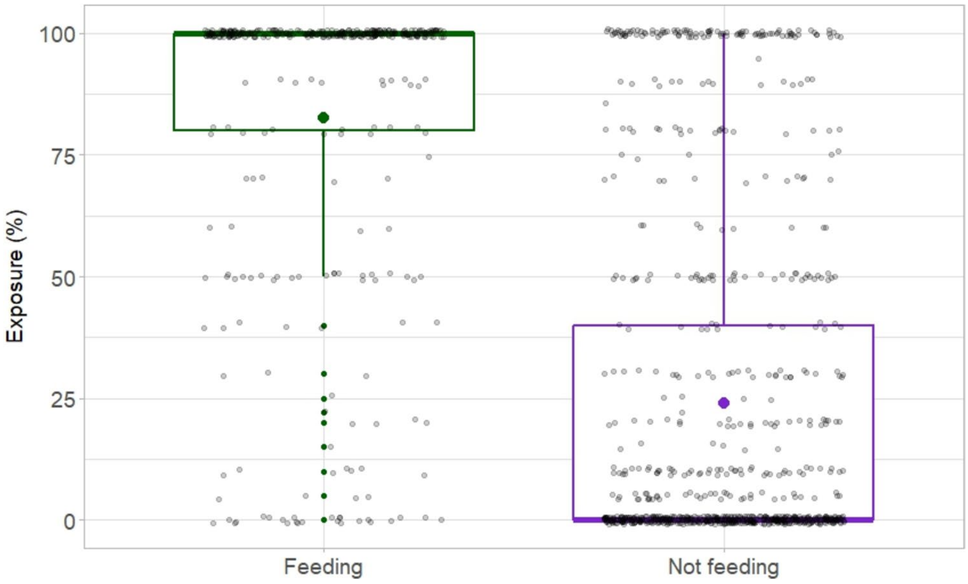
◂**Fig. 2** Box plots showing **a** detectability, **b** size, and **c** exposure of CoTS within each of the four distinct regions (see Fig. 1). Mean values are represented by the large coloured circular symbols. Each data point (grey jittered symbols) represents a SALAD survey for detectability and an individual CoTS for exposure. Detectability is calculated based on the ratio of recorded density to inferred density, where the latter included the number of distinct sets of feeding scars where CoTS were not detected. Exposure is the proportion (to the nearest 5%) of each individual starfish that is visible from directly above

CoTS using this survey method was estimated to be ~50%, assuming that there was at least one adult starfish within the immediate vicinity of all apparent feeding scars. Visual surveys based solely on sightings of individual CoTS are therefore likely to substantially underestimate local densities (see also Kayal et al. 2017). Our estimates of detectability were much lower than reported previously by autonomous divers (e.g. MacNeil et al. 2016; Kayal et al. 2017, Pratchett and Caballes 2025), which may be attributable to the method of estimating the true abundance. MacNeil et al. (2016) and Kayal et al. (2017) inferred the actual (true) density of CoTS based on recurrent sampling, and used much smaller sampling units, compared to our study. Critically, there are a proportion of CoTS that evade detection even during surveys conducted at night (MacNeil et al. 2016), and mark-recapture surveys cannot account for individuals that remain hidden within the reef matrix throughout recurrent surveys (typically conducted over 1–2 days). Detectability is therefore likely to be very sensitive to the size structure of local CoTS populations and corresponding changes in behavioural modality (Moran 1986). Indeed, our results demonstrate that CoTS detectability is highly variable and regionally structured, with significantly higher detectability in Cape Grenville and Lizard Island and lower detectability in Cairns and Princess Charlotte Bay. This regional pattern aligns closely with differences in average CoTS size, suggesting that strong size-based differences in behaviour of CoTS have a marked influence on detectability. MacNeil et al. (2016) demonstrated that detectability of smaller CoTS (<200 mm diameter) was less than half that of larger CoTS (>400 mm). Although starfish size could not be included directly in the detectability model due to unknown sizes of undetected individuals, the observed covariation between size and detectability supports prior findings that larger individuals are more active and more likely to be visible during daylight hours (Keesing 1995). Independent of size-based differences in behaviour, we also found that CoTS is much more likely to be feeding during the day in the far Northern GBR, which further contributes to regional differences in exposure and detectability.

Given limited detectability of CoTS and corresponding constraints in assessing absolute densities (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. Faure 1989; 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 conspicuous coral injuries. 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. coral bleaching). We contend that detectability reported in this study is most likely underestimated for two reasons: i) we do not (and cannot) account for detectability of feeding scars and ii) it was assumed that distinct clusters of feeding scars were caused by a single CoTS. There may also be additional CoTS concealed within the reef matrix without corresponding evidence of recent feeding activity, leading to over-estimates of detectability. We did not explicitly account for the proportion of CoTS that were detected without first sighting feeding scars, but there were very few instances (48 out of 1214) where no feeding scars were recorded within the immediate proximity of individual CoTS. Our sampling was intentionally biased toward searching for CoTS within the presence of feeding scars, which may negatively affect estimates of CoTS density, but are likely to positively affect estimates of detectability. Biases in our estimates of detectability are however, expected to scale with CoTS density, wherein it will be increasingly challenging to distinguish between distinct sets of feeding scars attributable to individual starfish. Accounting for feeding scars will, therefore, have greatest utility for resolving low to moderate densities of CoTS, which are very important for detecting and managing the initiation of population irruptions.

While CoTS hidden within complex reef habitats may be detected following extensive searching by autonomous divers, limited exposure greatly restricts the capacity to effectively survey CoTS using methods that are reliant on visual detection of CoTS from above (i.e., rapid fly-over surveys), such as manta tow and diver-independent camera systems (Lawrence et al. in review). Similarly, these methods provide limited opportunity to verify that apparent coral injuries are CoTS feeding scars (Lawrence et al. in review). Critically, this study shows that exposure of individual CoTS varies with size, but this pattern is not consistent among regions (Fig. 4; see also Burn et al. 2020), which will undermine accuracy and consistency of estimates of CoTS abundance obtained using rapid fly-over surveys. Regional variation in diurnal feeding behaviour and corresponding exposure is however only partly explained by differences in size structure, and more research is needed to understand why CoTS in the Far Northern GBR are found feeding more

Fig. 3 Box plot showing differential exposure of CoTS that were and were not feeding. Mean values are represented by the large coloured circular symbols. Each data point (grey jittered symbols) represents an individual starfish.



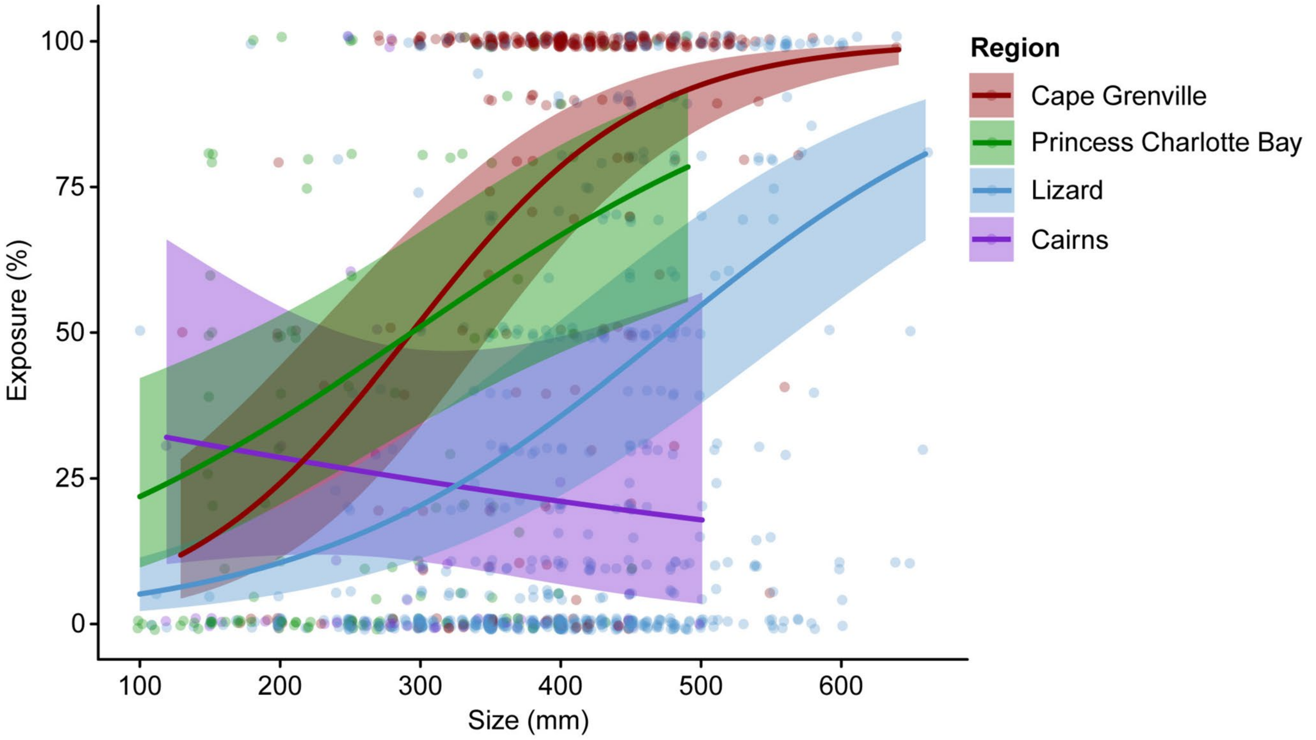


Fig. 4 Relationship between size (diameter, mm) versus exposure (%) of individual CoTS, specific to each region, based on predicted values for the best model (glmmTMB(cbind(Exposed,Hidden) ~ Feeding + Region × Size + (1 | ReefNo)). Each data point represents an individual starfish. Exposure is the proportion of the starfish (to the nearest 5%) that is visible from directly above.

often during the day are generally more exposed, regardless of size. Our study revealed marked increases in the exposure of CoTS with increasing body size, while overall exposure (independent of body size) was not significantly affected by the timing of surveys, though our surveys were only conducted during daylight hours. These findings confirm that most CoTS remain hidden during daylight hours (e.g. Ling et al. 2020), and it is only larger individuals that tend to be fully exposed during the day. Higher levels of CoTS exposure are recorded at night (De'ath and Moran 1998, Keesing 1995; Burn et al. 2020), providing potential opportunities to improve detectability for rapid fly-over survey methods, but this does not necessarily translate to higher levels of detectability for intensive diver-based methods (Pratchett and Caballes 2025).

Intrinsic size-based differences in the behaviour of CoTS have major effects on detectability and exposure (Keesing 1995; MacNeil et al. 2016; Burn et al. 2020). Most notably, this study reaffirms that emergence behaviour is closely tied to foraging activity (Ling et al. 2020). Ling et al. (2020) showed that individual starfish tend to remain hidden (within specific resting locations) for much of the day and only emerge to search for prey and feed. To feed on most corals, CoTS must sit atop the colony, necessitating that they are largely, or fully exposed. CoTS may however be concealed when feeding on the underside of tabular *Acropora*, on cryptic corals, or deep within large arborescent colonies. In this study, 70.24% of CoTS found feeding were fully exposed, and 86.06% were ≥ 50% exposed. The proportion of CoTS that was recorded feeding (30.47%) and fully exposed (29.90%) was similar to that of Keesing (1995), though exposure was strongly dependent on starfish size. Notably, most (57.73%) larger CoTS (> 500 mm diameter) were fully exposed, whereas most (61.77%) smaller CoTS (< 300 mm) were fully concealed. Changes in exposure with increasing size may account for sudden increases in the apparent densities of CoTS (which are generally apparent only when starfish reach 250–300 mm diameter; Chesher 1969; Pratchett et al. 2009), though these populations clearly arise from high densities of juvenile starfish (e.g. Zann et al. 1987), which are difficult to detect (but see Wilmes et al. 2020). Early detection of new and renewed population irruptions of CoTS, which is fundamental for timely and effective suppression of CoTS densities (Matthews et al. 2024), is therefore reliant on maximising detection of smaller size classes.

Aside from intrinsic factors that affect detectability and exposure, the effectiveness of sampling CoTS is likely to be moderated by habitat structure and environmental conditions (MacNeil et al. 2016). Notably, Keesing (1995) showed that the proportion of CoTS that was exposed during the day was lowest in shallow (< 3 m depth) reef habitats but increased with water depth (to 9 m depth). In the current study, neither zone nor depth significantly improved models for detectability and exposure. There was also no effect of coral cover on detectability (see also MacNeil et al. 2016; Burn et al. 2020), although the best fitting model also included habitat complexity, with detectability decreasing in more complex reef structures. Although this effect was not statistically significant, it is ecologically plausible and consistent with previous research showing that complex habitats will presumably provide CoTS with increased opportunity to seek refuge within the interstices of the reef matrix, and thereby evade detection (Chandler et al. 2023). Interestingly, high coral cover did not necessarily afford CoTS the same opportunity, suggesting that they tend to seek refuge within the reef matrix, rather than within or beneath living corals. Conversely, areas with low habitat complexity, especially those tending toward almost flat unstructured reef platforms, provided limited opportunity for CoTS to remain undetected. Sustained degradation of coral reef ecosystems, including declines in topographic complexity (Wilson et al. 2010), may therefore lead to changes in detectability and presumed abundance of CoTS.

Acknowledging inherent biases and constraints of different survey methods, and corresponding estimates of CoTS densities, is increasingly important given that management decisions are often based on absolute density thresholds (e.g. Westcott et al. 2020; Rogers et al. 2023; Matthews et al. 2024). Our results show that detectability using SALAD surveys is rarely > 50%, even under optimal conditions, and is especially low in habitats with smaller, more cryptic CoTS or structurally complex reef matrices. Survey methods must account for both behavioural and environmental constraints on detection. The capacity to effectively resolve low-to-moderate densities of CoTS is also fundamental in understanding when, where and why population irruptions arise (Pratchett et al. 2014). It is essential therefore, that sampling and monitoring programmes designed to support (and assess the effectiveness of) management approaches, use survey methods that provide necessary levels of detection and resolution. We are not suggesting that there is any need to rationalise or standardise survey methods (see also Lawrence et al. in review). Rather, it is important to recognise that different methods have different purposes or applications and do not necessarily provide complementary information. SALAD surveys provide practical and scalable opportunities to sample over relatively large expanses of reef habitat (cf. transect-based sampling) without forsaking the capacity to search intensively as necessary (cf. manta tow surveys), both to verify that conspicuous coral injuries represent CoTS feeding scars and maximise detection of individual CoTS.

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Author contributions MSP, PCD, and CFC conceived and designed the study. All authors contributed to collecting the data. MSP analysed the data. MSP and PCD wrote the manuscript, and all authors provided feedback and approved the final manuscript.

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Data availability SALAD data are available via eATLAS data repository (https://eatlas.org.au/datasets; Pratchett et al. 2026), or from the corresponding author upon request.

Declarations

Conflict of interest Morgan Pratchett is EIC of Coral Reefs, and Ciemon Caballes is guest editor for the current Special Issue, but neither had any role in the peer review and publication decisions regarding this manuscript.

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