



Ecological analyses to inform management targets for the culling of crown-of-thorns starfish to prevent coral decline

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Abstract The crown-of-thorns starfish (COTS), *Acanthaster cf. solaris*, is one of the main contributors to declines in coral cover on the Great Barrier Reef (GBR) and remains one of the major acute disturbances on coral reefs throughout much of the Indo-Pacific. Extensive control programs on the GBR involve manual culling of COTS in the field, and research is needed to inform these management efforts. Data from the Great Barrier Reef Marine Park Authority's (GBRMPA) COTS control program provide near-real-time CPUE (Catch-Per-Unit-Effort, COTS culled per minute) data ideal for operational decision-making but these must be converted to density estimates before they can be related to ecological status of reefs or incorporated into ecological models. We developed conversions between common COTS field survey methods (i.e. manta tow, SCUBA transect searches) and COTS control program CPUE data using estimates of sightability and detectability. We used a population model and COTS size-structure data from COTS control program culling efforts to estimate that, on average, only 19% of 1-yr-old COTS

(1–15 cm) are available to be culled. Finally, we developed a CPUE-COTS density relationship to estimate the threshold levels of COTS that prevent net growth of hard corals. Culling programs should therefore aim to achieve CPUEs below these ecological thresholds in order to effectively promote coral growth and recovery. These ecologically sustainable thresholds of COTS density varied depending on hard coral cover. For example, for 35% fast-growing coral cover, COTS culling needs to continue until CPUE decreases to below 0.05 COTS/min (1 COTS per 20 min) in order to prevent coral decline, whereas if coral cover is higher (80%), then a higher target threshold CPUE of ca. 0.08 COTS/min (ca. 3 COTS per 40 min) may be ecologically sustainable. These estimates underpin the current pest management rules being implemented by the GBRMPA in its COTS control program.

Keywords *Acanthaster cf. solaris* · Great Barrier Reef · Ecological threshold · Pest management · COTS · Culling · Coral reef

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Introduction

The crown-of-thorns starfish (COTS), *Acanthaster cf. solaris*, is one of the main contributors to declines in coral cover on Australia's Great Barrier Reef (GBR) and remains one of the major acute disturbances on coral reefs throughout much of the Indo-Pacific (Pratchett 2010; Fabricius et al. 2010; De'ath et al. 2012). COTS feed primarily on scleractinian corals, and occur on reefs across the tropical and sub-tropical Indo-Pacific (De'ath and Moran 1998). They are mostly rare (~ 1 COTS·ha⁻¹) but, under certain circumstances, can undergo dramatic increases in density (termed outbreaks; reaching $> 10,000$ COTS·ha⁻¹)

(Pratchett et al. 2017). Several hypotheses have been proposed to explain the occurrence of these outbreaks (reviewed by Pratchett et al. 2017), including their life history and phenomenal reproductive capacity (Babcock et al. 2016), and anthropogenic changes in environmental conditions, namely the ‘terrestrial run-off hypothesis’ (Birkeland 1982) and ‘predator removal hypothesis’, (Endean 1969). Although single factors (e.g., elevated nutrients (Birkeland 1982)), or the life history traits of *Acanthaster* alone (Birkeland 1989), could be a major driver under some circumstances, most researchers concur that it is unlikely that a single factor explains the diverse incidences of crown-of-thorns outbreaks (Pratchett et al. 2017). Impacts from climate change are also adding to the degradation of coral reefs globally (Claar et al. 2018; Hughes et al. 2018a, b) highlighting the urgent need to take action to mitigate coral decline.

An “outbreak” state has been quantitatively defined when a COTS population consumes corals at a rate which is greater than the coral growth rate; thought to occur when densities exceed 10 individuals ha^{-1} (> 1000 COTS km^{-2}) (Birkeland and Lucas 1990; Moran and De’ath 1992; Keesing and Lucas 1992). With the fourth recorded outbreak of COTS since the 1960’s now occurring on the GBR, control of COTS across reefs is regarded as one of the most feasible on-ground actions managers can take to prevent coral decline given that the other major causes of decline are bleaching and cyclones (De’ath et al. 2012; Fletcher et al. 2020; GBRMPA 2020).

Many methods have been used throughout the years and across the Pacific to directly control COTS populations on a local scale, such as manual removal and burial ashore, cutting them up, and injections of toxic chemicals (Boström-Einarsson and Rivera-Posada 2016). More recently COTS culling methods have been revolutionised through the use of a highly effective method involving a single small volume injection of oxbile (Rivera-Posada et al. 2014). This discovery paved the way for the current broad-scale COTS control program on the Great Barrier Reef, because it enabled divers to cull COTS more efficiently than before. However, research was needed to support these control efforts and inform the culling targets that would keep local COTS populations below outbreaking threshold levels, in order to achieve the management objective of mitigating coral decline. A method was therefore needed to enable comparison between culling rates (as an index of COTS abundance) and outbreak thresholds.

Since 2012, considerable resources have been invested by the Australian Government into a broad scale and coordinated COTS control program, which is managed by the Great Barrier Reef Marine Park Authority (GBRMPA). The COTS control program aims to reduce the damaging impacts of COTS on coral populations across individual

reefs in the Marine Park that are valuable for the resilience of the ecosystem and the industries it supports (GBRMPA 2020). From 2012 to 2018, control effort was focused at the spatial scale of individual sites (average size 20–30 ha) on these high-value reefs. In 2018, control effort was expanded to manage COTS populations across the entire extent of high-value reefs accessible to divers (Fletcher et al. 2020). As part of this program, hard coral cover at high-value reefs is estimated using Reef Health and Impact Surveys (RHIS) in order to inform control efforts (Fletcher et al. 2020).

In addition to local direct control of COTS through culling, management also includes preventative long-term approaches to mitigating outbreaks (GBRMPA 2020) such as reducing nutrient inputs into the GBR lagoon (Fabricius et al. 2010) and protecting the natural predators of COTS using a zoning plan that limits fishing activities (Sweatman 2008; Vanhatalo et al. 2016).

The aim of this study was to explore important ecological thresholds for COTS populations in relation to potential for population growth and available food sources (coral cover) (Babcock et al. 2014). Knowledge of these thresholds is informing the management of COTS, which involves a comprehensive surveillance and culling program (Fletcher et al. 2020). To support management efforts, we used a range of modelling methods as well as analyses of available empirical data.

We use a multi-species model to estimate ecological thresholds for COTS, being the levels above which COTS densities are considered to be outbreaking and cause declines in coral cover. Our analysis takes into account that COTS are impacting a range of sites that have different levels of coral cover and focuses on estimating the point at which the net growth rate in coral cover is zero. In other words, for a given coral cover level, we estimate the COTS density where coral cover stays constant due to coral growth being balanced by COTS consumption. Such densities are desirable and correspond to being below the outbreak threshold for the specified coral cover level. We compare model results with empirical findings and utilise COTS control program culling data for comparison.

The category of models we base our analyses on, “Models of Intermediate Complexity for Ecosystem assessments” (MICE), has a tactical focus, including use as ecosystem assessment tools (Plagányi et al. 2014a). MICE are context- and question-driven and limit complexity by restricting the focus to those components of the ecosystem needed to address the main effects of the management question under consideration. MICE estimate parameters through fitting to data, use statistical diagnostic tools to evaluate model performance and account for a broad range of uncertainties. These models therefore address many of the impediments to greater use of ecosystem models in

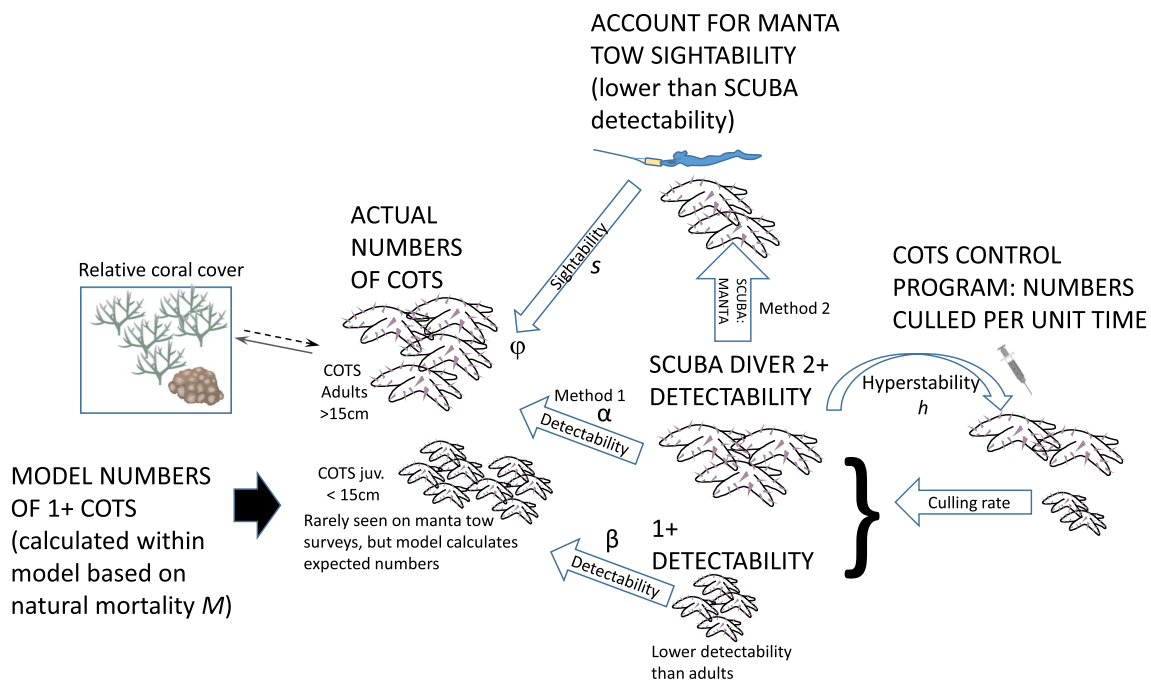


Fig. 1 Summary of process used to convert between actual and modeled number of COTS, using field data from SCUBA counts, manta tow counts and COTS control program culling CPUE (COTS/min), showing parameter definitions as in Table 2

strategic and particularly tactical decision-making for marine resource management and conservation (Plagányi et al. 2014a), and are increasingly being used to support implementation of ecosystem-based management (Townsend et al. 2019).

Our approach has several advantages compared with analyses of empirical data alone: the model is dynamic rather than needing to be based on static snapshots; the model is continuous and hence can smoothly inform on changes in coral cover as a function of COTS abundance; the model is able to capture alternative coral-COTS compositions and link smooth multidimensional and nonlinear changes between states to the relative change in the composition of the system; the model integrates available life history information in a manner consistent with observed data rather than attributing discrete coral cover measures to COTS population abundance at a point in time; and the model is able to rigorously estimate coral-COTS interaction parameters and use these to derive plausible rates of change in coral cover as a function of both COTS density and coral cover. The approach used is therefore akin to that widely used to provide science-based advice for exploited populations, using integrated modelling approaches incorporating all available data, with explicit representation and estimation of uncertainty (Maunder and Punt 2013). However, as per any model or approach—empirical or otherwise—we acknowledge the reliability of model outputs is strongly contingent on the quality of data used as inputs.

As ecological thresholds underpin many of the COTS monitoring and control activities, there is a need to be able to use established relationships to convert between different estimates of density, such as obtained from manta tow survey and diver SCUBA-based transect estimates (cf Fernandes et al. 1990). These estimates differ from the true total abundance because of the difficulties in observing very small cryptic COTS. However, models can be used to estimate the numbers of small unobserved COTS. In addition, there is a need to convert the COTS density estimates to CPUE (Catch-Per-Unit-Effort or COTS culled per dive minute) measures so that they can be directly applied by control teams in the field. Hence, we derive relationships between different COTS density measurements estimated through common COTS survey techniques (i.e. manta tow, transect surveys) and CPUE as recorded by divers undertaking culling operations (Fig. 1).

Methods

COTS-coral model

The equilibrium (static) analysis to compute equilibrium COTS-coral interaction solutions is based on a MICE describing the interaction between COTS and two groups of coral (Morello et al., 2014). The full equations, list of variables and parameter estimates and input values are as per Morello et al. (2014) and are given in Online Resource

1 (Tables S1–S3). In line with MICE principles (Plagányi et al. 2014a), the model constrains complexity by restricting focus to two aggregated groups of corals—fast-growing corals (*Acropora* spp.), and massive slow-growing corals (e.g. Faviidae, massive *Porites* spp. etc.) and how COTS interact with them (Online Resource 1: Table S1). The model was fitted to manta tow and scuba transect survey data from Lizard Island (Queensland, Australia), collected by the AIMS LTMP from 1994 to 2011 for both COTS and coral cover (Sweatman et al. 2008).

The coral dynamics are described using logistic population models. Consequently, they assume that the population rate of change depends on the biomass. COTS preferentially feed on the fast-growing coral species and switch to consuming the slower-growing massive corals only when these corals occur in relatively high densities and/or when fast-growing corals have been depleted (Birkeland and Lucas 1990). In the model, COTS therefore start by consuming fast-growing corals and increasingly supplement their diet with slow-growing corals as the density of fast-growing coral declines (Online Resource 1: Table S1). The two coral categories have different growth rates as well as different rates of consumption by COTS (Online Resource 1: Tables S1, S4). To assess the robustness of model results to different coral growth rates, we include in our results two sensitivity analyses that assume higher and lower fast-growing coral growth rates (Online Resource 1: Table S4).

COTS populations were modelled through an age-structured approach. Here individuals belong to one of three age classes—0, 1 or 2+ (Table 1)—where the oldest class is an absorbing state. Parameters relating to COTS recruitment, mortality and their inter-specific interactions with coral were estimated. The number of age-0 COTS (or “recruits”—COTS in their first year of life) can be modelled as self-recruitment (based on a stock-recruitment relationship) and immigration (the number of settling larvae transported to the region from elsewhere) (Eq. 1a, Online Resource 1: Table S1). The stock-recruitment relationship is a statistical description of the average of several biological processes such as competition and density dependence (Hilborn and Walters 2001). It is a useful formulation for capturing changes in self-recruitment rates as a function of changes in density. Total recruitment also accounted for the density-independent phenomenon of

immigration, with the magnitude of an immigration pulse estimated by fitting to available data (i.e. the observed increase in recruitment was estimated as a combined effect of density-dependent and density-independent processes). The model-estimated natural mortality rate of 2.6 y^{-1} (with associated Hessian-based confidence interval $2.3\text{--}2.8 \text{ y}^{-1}$) is high but not unexpected given that it is estimated as the average rate (and thus accounts for the relatively higher rate expected for younger age classes) and is also an integrated parameter to account implicitly for all sources of natural mortality. The latter could include pathogenesis which may increase in response to prey depletion and deteriorating condition of adult starfish (Pratchett et al. 2017). The representation of inter-specific interactions involves adding a multiplier for survival or breeding success based on the relative depletion of the prey.

The robustness of the COTS-coral model formulation and parameter estimates is demonstrable through the work of Condie et al. (2018). Here, the MICE model and associated parameter estimates have been embedded in the CoCoNet model (Condie et al. 2018) which resolved a large network of individual reefs and was able to successfully simulate realistic successive COTS population outbreaks as an emergent property of the model.

Equilibrium COTS-coral equations

The fast-growing coral equation from Online Resource 1: Table S1 can be rearranged and solved for the case of zero change in coral biomass (cover) as follows (where variable definitions are listed in Online Resource 1: Table S2):

$$r^f C_\infty^f (1 - C_\infty^f / K^f) = (1 - \rho_y) \frac{p_1^f (N_{\infty,1} + N_{\infty,2}) C_\infty^f}{1 + \exp(-(N_{\infty,1} + N_{\infty,2}) / p_2^f)} \tag{1}$$

where $C_\infty^f, N_{\infty,1}, N_{\infty,2}$ denote equilibrium fast-growing coral cover, number of age-1 and number of age 2+ yr COTS, respectively, and K^f is the fast-growing coral carrying capacity.

Substituting for ρ_y , this simplifies to:

$$\frac{r^f (1 - C_\infty^f / K^f)}{e^{(-5C_\infty^f / K^f)}} = \frac{p_1^f (N_{\infty,1} + N_{\infty,2})}{1 + \exp(-(N_{\infty,1} + N_{\infty,2}) / p_2^f)} \tag{2}$$

Table 1 Age-size-life-stage equivalence assumed for COTS in this study and in the MICE model (Morello et al. 2014), based on Pratchett (2005, 2010) and Pratchett et al. (2014)

| Age | Size (diameter, mm) | Stage | Age class used in MICE model |
|--------------|---------------------|---------------------------------|------------------------------|
| 11+ d | 0.5 | Newly settled juvenile | |
| 0.5–6 months | 1–10 | Algal feeding juvenile | Age 0 |
| 0.5–2 yrs | 10–150 | Coral-feeding juv. to sub-adult | Age 1 |
| > 2 yrs | > 150–350 | Coral-feeding adult | Age 2+ |

Table 2 Parameter values used for base threshold calculations as well as a number of sensitivity tests

| Parameter description | Symbol | Method 1 | Method 2 | Sensitivity 2 | Sensitivity 3 | Sensitivity 4 | Sensitivity 5 |
|---|----------|--------------------|-------------------------|-------------------------|-------------------------|--------------------------|---------------|
| Manta tow area (ha) | <i>A</i> | 0.2 ² | 0.2 | 0.2 | 0.2 | 0.2 | 0.15 |
| Model-estimated COTS mortality rate (yr ⁻¹) | <i>M</i> | 2.56 ³ | 2.56 | 2.56 | 2.56 | 1.76⁸ | 2.56 |
| Model survey parameter | <i>φ</i> | 0.946 ³ | 0.946 | 0.946 | 0.946 | 1.276⁸ | 0.946 |
| Manta tow sightability (2+ COTS) | <i>s</i> | – | 0.23⁵ | 0.45⁶ | – | – | 0.45 |
| Culling detection 2+ (> 15 cm) | <i>α</i> | 0.82 ⁴ | 0.82 | 0.82 | 0.82 | 0.82 | 0.82 |
| Culling detection 1-yr-old (< 15 cm) | <i>β</i> | 0.19 ¹ | 0.19 | 0.19 | 0.34⁷ | 0.19 | 0.34 |
| CPUE hyper-stability parameter | <i>h</i> | 0.5 ¹ | 0.5 | 0.5 | 0.5 | 0.5 | 0.5 |
| CPUE-density scalar | <i>q</i> | 0.669 ¹ | 0.669 | 0.669 | 0.669 | 0.669 | 0.669 |

Bold text indicates the main change from the Method 1 scenario

Source: 1-this study; 2- Miller et al. 2009; 3-Morello et al. (2014); 4-MacNeil et al. (2016); 5-Fernandes et al. (1990); 6-Fernandes (1990); 7-Updated 1 + detection (Online Resource Table S5); 8- Plagányi et al. (2014a)

where $r^f = 0.5$ (input); $p_1^f = 0.129$ (std 0.041) (estimated within the model—Morello et al. (2014)) $p_2^f = 10$ (fixed input).

For different values of coral depletion (C_∞^f/K^f), a Newton–Raphson root-finding method is then used to solve for the number of COTS aged 1 yr and older ($N_{\infty,1} + N_{\infty,2}$) that keeps the coral in equilibrium at a pre-specified level. The age 2+ yrs group includes all COTS aged 2 yrs and older, and is related to the abundance of age-1 individuals via:

$$N_{\infty,2} = \frac{N_{\infty,1} e^{-M}}{1 - e^{-M}} \tag{3}$$

The total number of COTS is $N_\infty = N_{\infty,1} + N_{\infty,2}$ and this can be further separated into the number of age 1 and 2+ COTS using the relation:

$$N_{\infty,2} = e^{-M} N_\infty \tag{4}$$

$$N_{\infty,1} = N_\infty - N_{\infty,2} \tag{5}$$

where the best-fit estimate of natural mortality M is 2.56 y⁻¹ (with Hessian-based standard error 0.15). A lower estimate of M of 1.708 y⁻¹ (SD = 0.28) from Plagányi et al. (2014b) is also used as a sensitivity (Table 2).

Similarly, for the slow-growing coral, the following equation can be used to solve for the number of COTS that keeps the coral cover in equilibrium, except that this is simultaneously a function of the depletion level of the fast-growing coral (because of the switch function – Eq. 7 in Online Resource 1: Table S1):

$$\frac{r^m (1 - C_\infty^m/K^m)}{p_1^m (1 + e^{-5C_\infty^f/K^f})} = \frac{(N_{\infty,1} + N_{\infty,2})}{1 + \exp(-(N_{\infty,1} + N_{\infty,2})/p_2^m)} \tag{6}$$

The number of COTS that keep slow-growing coral in equilibrium is therefore solved for a range of different steady state fast-growing coral depletion levels.

Converting modelled COTS numbers to equivalent densities seen by divers

The model numbers of 2+ yr COTS are fitted to data from manta tows (COTS · manta tow⁻¹), and a survey proportionality parameter ϕ is estimated in the model. The model assumes no age-1 COTS are observed by manta tows as very few small COTS are recorded (Miller et al. 2009). Manta tows involve towing an observer behind a tender vessel at a constant speed for 2 min, which covers approximately 200 m of reef habitat (Moran and De’ath 1992; Miller et al. 2009; Vanhatalo et al. 2016). The towed observer counts all COTS visible within a 10 m search width along the tow path suggesting each manta tow survey covers an area (A) of approximately 0.2 ha. Manta tows are designed to estimate relative abundance rather than absolute abundance as the latter is complicated by the cryptic nature of COTS and hence availability bias (Fernandes et al. 1990; Moran and De’ath 1992).

Another common method for estimating COTS abundance in the field is through SCUBA transects involving divers systematically searching along a transect with pre-specified length and width. Although manta tows are useful for quickly collecting information on relative COTS numbers across a broad spatial scale, SCUBA transect observations are more accurate at estimating COTS numbers because when on SCUBA, observers have the opportunity to search for smaller and more cryptic individuals (Fernandes et al. 1990). Hence the COTS densities recorded using manta tow surveys (termed the sightability s) are substantially lower than SCUBA observations, for which we define detectability of 2+ yr COTS as α and 1-yr COTS as β , noting that most GBR SCUBA transect observations in the literature have zero detectability of 1-yr-old starfish (i.e. < 15 cm). Comparisons between manta-towed and SCUBA transect (20 m x 10 m) observations suggest that fewer COTS are counted on manta



tows, such that the so-called sightability s is less than 23% on average (Fernandes et al. 1990). However, sightability is maximised at search widths of 9 m ($s = 45\%$), improves at higher densities and bias can be mitigated using other indices such as feeding scars (Fernandes 1990). Here we assume the COTS control program cull divers have a similar detectability bias (α) to SCUBA transect divers and compute their detectability (β) of small COTS based on available data.

A mark-recapture type field study to estimate detectability suggested that α for adult COTS (equivalent to 2+ yr COTS described in this study) was 82% [with 95% uncertainty interval 77–87%] (MacNeil et al. 2016). No comparison is available for the 1-yr-old detectability as smaller COTS were not observed in the MacNeil et al. (2016) study.

Below follows a summary of the two methods used to convert model-estimated COTS densities to manta versus SCUBA transect densities and hence to the densities encountered by cull divers and their associated CPUE (Table 2). Two methods for converting starfish densities to those encountered during cull dives are included to encapsulate potential alternative structures of the conversion relationship. We use model estimates (Eqs. 4 and 5) of the actual abundance scaled to units of COTS per hectare (cull program outputs are expressed in terms of COTS/ha), and assuming the population is in equilibrium so that we can compute the relative proportions of 1-yr and more than 2-yr-old COTS, denoted here as N_1 and N_2 , respectively.

1. Method 1 applies the 2+ yr detectability estimate α from MacNeil et al. (2016) to convert modelled starfish numbers (actual per hectare) to SCUBA observed densities and assumes that CULLING 2+ yr observed densities are the same as the SCUBA transect densities:

$$N_2^{\text{cull}} = \alpha \cdot N_2 \quad (7)$$

2. Method 2 is an alternative that uses the relationship of Moran and De'ath (1992) to directly convert manta tow observed densities (MC) to SCUBA transect (SC) observed densities (see also Haywood et al. 2019). To obtain manta tow densities from modelled starfish numbers, as well as the model scaling parameter estimate φ , manta tows are assumed to cover an area (A) with s sightability of 2+ yr COTS:

$$\text{MC} = s \cdot \varphi \cdot N_2 \quad (8)$$

From which SCUBA observed densities are calculated (Haywood et al. 2019):

$$\sqrt[3]{\text{SC}} = 0.8071 + 1.2008 \times \text{MC}^3 \quad (9)$$

Again, assuming that the culling program 2+ yr observed densities of 2+ yr COTS are the same as the SC densities consequently yields:

$$N_2^{\text{cull}} = \alpha \cdot \text{SC}/A \quad (10)$$

3. The contribution of 1-yr COTS to total culling numbers (1-yr and 2+ yr COTS) is calculated via the detectability of 1-yr COTS based on the culling data (data as described below), and hence total numbers as follows:

$$N^{\text{cull}} = \beta N_1 + N_2^{\text{cull}} \quad (11)$$

4. A relationship is established between COTS density and CPUE (see below) in order to convert culling density observations to CPUE with units of (N^{cull} COTS)/min which is the measure that is most directly comparable to field CPUE measures (i.e. it accounts for the size distribution of COTS removed in the field).

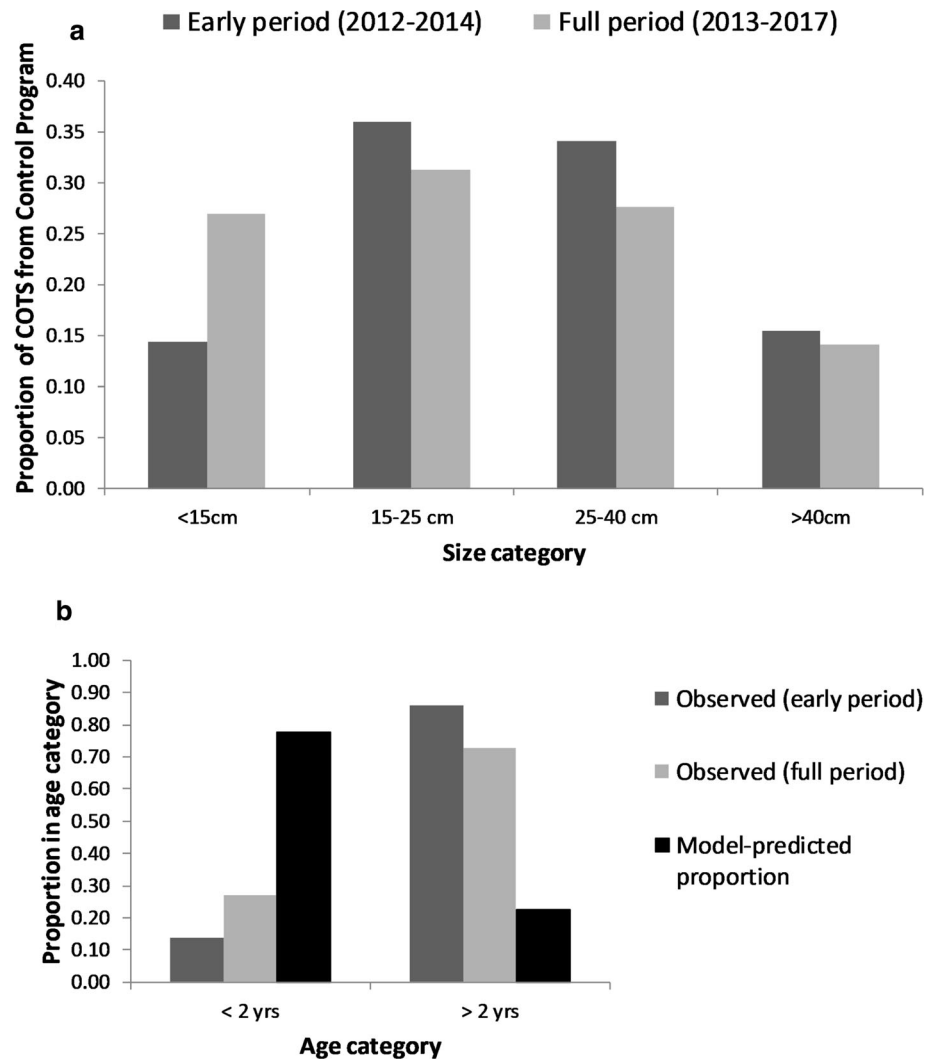
Alternative sensitivity analysis parameter values used in calculations are shown in Table 2.

Comparing model results and COTS control program data

We used the COTS control program size structure data collected during culling to compute an average size structure, in turn roughly converted to an age distribution. We compared this distribution to the model-derived expected distribution of COTS actually present in the field (assuming stable growth), with culling data. The cull data includes specification of size classes as follows: < 15 cm (age 1); 15–25 cm (age 2+); 25–40 cm (age 2+) and > 40 cm (age 2+).

These sizes correspond to the age classes in Table 1 which are based on Pratchett (2005, 2010) and Pratchett et al. (2014). Thus, to apply an age-size split, we assume the categories < 15 cm to COTS that are less than 2 yrs old, whereas the three larger categories correspond to age 2+ yr COTS. Small COTS individuals can be cryptic, so it was determined that COTS less than 10 cm were more difficult to find. Given the lower size category extends to < 15 cm we would like to know the relative proportions of 1-yr-old and 2+ yr COTS culled as part of the control program (Fig. 1). We therefore summed all the length frequency data from removals during 2012–2014 from all reefs and computed the average size (and age) distribution as shown in Fig. 2 and Online Resource 1: Table S5. COTS control program divers likely cull most 2+ yr COTS, but the proportion of the 1-yr COTS culled is not known hence we defined a detectability proportion β for this age class.

Fig. 2 (a) Summary of the size distribution of COTS culled based on COTS control program data available when the first model was constructed (2012–2014) compared with a sensitivity using updated data for the full period (2013–2017), and (b) conversion to relative age proportions for comparison with model-derived age distribution representing theoretical “true” distribution in the field



Based on an estimate of natural mortality, we can use Eq. 3 above to predict the number of 2+ yr COTS corresponding to any number of 1-yr-old COTS and hence what the average COTS age distribution should be. We substituted our base-case estimate ($M = 2.56 \text{ y}^{-1}$) as well as two sensitivities ($M = 1.708 \text{ y}^{-1}$; $M = 1.461 \text{ y}^{-1}$; Plagányi et al. 2014b). This suggests that the expected relative percentage of 1-yr-olds compared to 2+ yrs COTS ranges from 77% to 92% (Online Resource 1: Table S5). But the proportion of 1-yr COTS culled is only 14.4% of total observed numbers (over 2012–2014). This low percentage is because as expected, divers will “miss” many 1-yr aged COTS. Accordingly, we derived an estimate of the detectability of the 1-yr-old COTS by calculating what percentage of the expected 1-yr-olds are observed, i.e. $\beta = 14.4/77$ which gives $\beta = 19\%$ (or using a higher expected percentage of 92%, this gives $\beta = 16\%$). We used $\beta = 19\%$ as our base-case detectability estimate but also did an additional sensitivity test as below.

At the time of the initial analysis to provide guidance for management, COTS control program size structure data were available for the period 2012–2014 and were used to compute an average size structure, in turn roughly converted to an age distribution (Fig. 2). A more recent analysis using updated control program data for the period 2013 to 2017 from a subset of reefs (Online Resource 1: Table S5) indicated a higher percentage (26.9%) of 1-yr-old COTS being killed. Substituting as above (i.e. $\beta = 26.9/77$) suggested a higher detectability estimate of 1-yr COTS ($\beta = 34\%$) (Fig. 2), possibly because of the efficient prior culling of larger COTS and also potentially improved skills in the detection of small COTS. Given the challenges in estimating detectability, we used both our high ($\beta = 34\%$) and low ($\beta = 19\%$) estimates in our analyses.

CPUE-COTS relationship

The relationship between CPUE (measured as COTS culled per minute) and COTS density is unlikely to be linear as searching and handling time constraints will mean that at high COTS densities, there is an upper limit to the number of COTS that can be culled per unit time. Hence it is more likely that the relationship is a hyper-stable one, supported also by the fact that a hyper-stability relationship is the most common form of relationship used in fisheries to describe non-proportionality between CPUE and abundance in cases where CPUE remains high while abundance declines (Harley et al. 2001).

The relationship between COTS culled and total COTS density was assumed to be:

$$CPUE_t = q(N_t^{\text{cull}})^h \quad (12)$$

where $CPUE_t$ is the number of adult COTS culled per unit of effort at time t , q is the catchability coefficient (the proportion of the total COTS population culled using the removal method in question), N_t^{cull} in this application represents the COTS population (> 11 cm) at time t in the water as counted by Fisk and Power (1999) (see below), and h is the hyper-stability coefficient determining the shape of the relationship (note that $h = 1$ implies a linear relationship, $h = 0$ no relationship).

In order to fit the above equation to available data, we developed a model in AD Model builder (Fournier et al. 2012) and its estimation routines were used to estimate the parameters of this relationship and compute Hessian-based standard error estimates to assess the precision with which the parameters are estimated. The model was run using fixed values of h and estimating q , as well as attempting to estimate both q and h .

The model was fitted to culling data collected by Fisk and Power (1999). They comprise catch per unit effort (COTS removed·h⁻¹) and COTS density estimates (COTS·ha⁻¹). These data were collected from two small reefs around Lizard Island between October 1995 and August 1996 and each reef was visited weekly for the first 10 weeks and then every 2 weeks for the following 20 weeks. The culling method involved injections of sodium bisulphate, which requires 10–20 injections per starfish to be effective. On each visit the injection effort was a standard of 2 person hours. COTS densities were estimated every four months (four times within the period) by 50x5m belt transects, before COTS were removed and hence only eight data points are available for the calibration. Because the culling method used in Fisk and Power (1999) required 10–20 injections per starfish it was less efficient than the single-shot injection of oxbile currently used in the COTS control program. Consequently, the CPUE estimates from Fisk and

Power (1999) are likely to be lower than the current CPUE values, but the bias is a conservative one as aiming for a lower CPUE increases the chances of COTS being sufficiently reduced to allow coral growth.

We also considered results from a study by MacNeil et al. (2016) which were not available at the time of the initial analyses. They found a hyper-stable relationship between CPUE and known density based on mark-recapture methods and estimated a hyper-stability parameter of 0.33 [confidence interval: 0.21, 0.46] (MacNeil et al. 2016). However, they focused only on larger COTS plus recorded densities were substantially higher (starting from 250 large COTS/ha) than those being considered for analysis of low threshold levels, and we were unable to successfully extrapolate their results to the scale needed.

Applying the CPUE-COTS relationship to model results

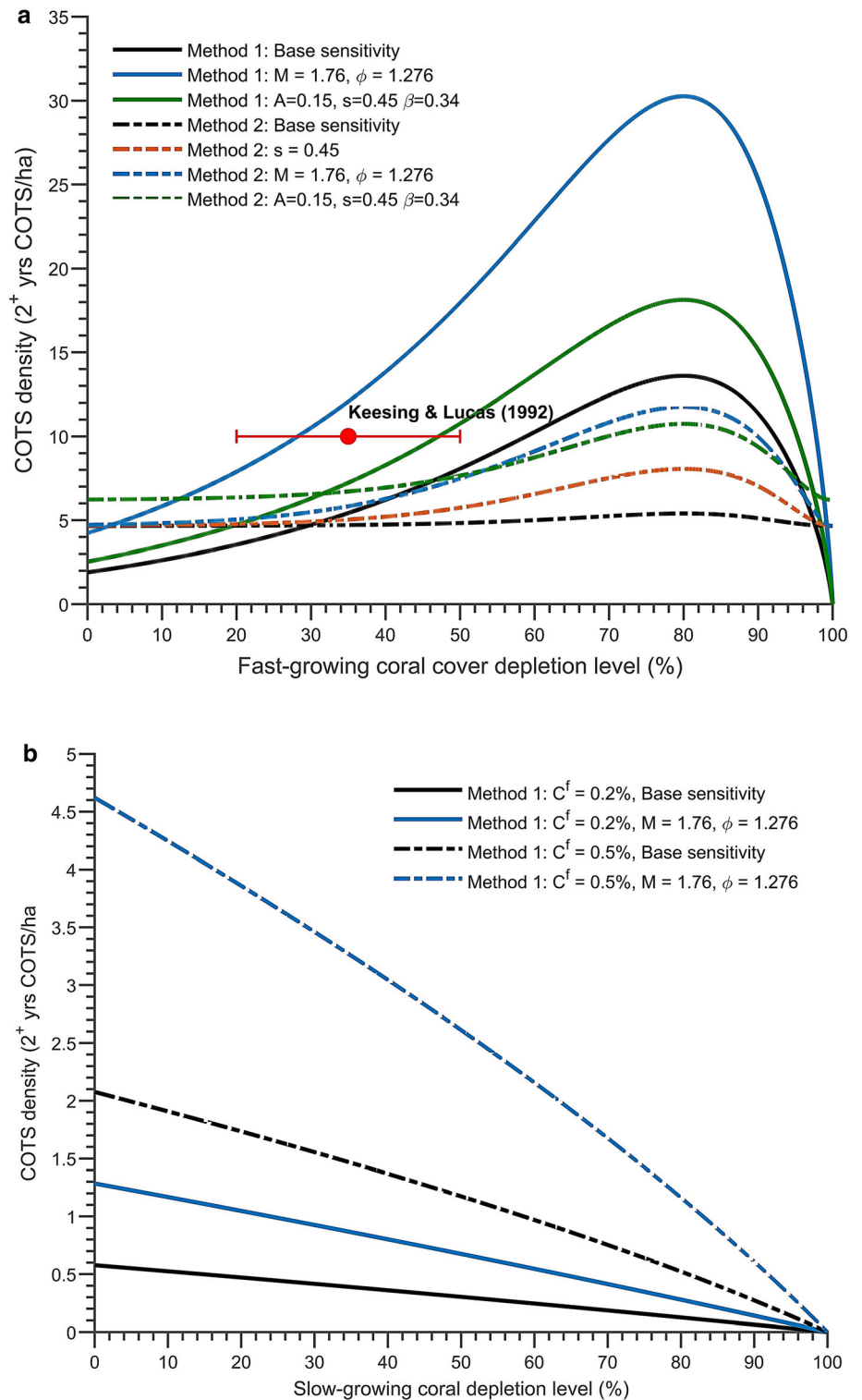
Using the best-fit model ($h = 0.5$), the CPUE-COTS relationship was used to translate COTS biomass into CPUE in the same units as used operationally by vessels in the COTS control program, i.e. total COTS/min. As the proportion of < 15 cm COTS recorded in the culling data has changed over time (Fig. 2), density and comparable COTS numbers are also presented in terms of numbers of 2+ yrs COTS only.

Results

COTS-equilibrium coral relationship

The point at which COTS consumption of coral outstrips coral growth is key to the ecology and management of the relationship between COTS and corals on coral reefs. Figure 3 shows the number of COTS (2+ yrs COTS·ha⁻¹) that equilibrate (A) fast-growing (*Coralf*) and (B) slow-growing (*Coralm*) coral growth for coral cover at a range of levels as shown. Values for COTS at levels below the curves are sub-outbreak densities, that is the rate of consumption of corals by COTS is below the net growth rate of the coral assemblages. Model results are compared with the outbreak threshold (10 COTS·ha⁻¹; COTS > 20 cm i.e. 2+ yr COTS) defined by Keesing and Lucas (1992) for cover of fast-growing coral (*Coralf*) in the range 20% to 50%, and there is excellent agreement between the results across this range of coral cover (Fig. 3a). The number of COTS required to cause a net reduction in coral cover declines near minimum and maximum values because coral cover is constrained by the 0 and 100% bounds. In this context coral assemblages with approximately 80% cover of fast-growing coral shows the greatest resistance to COTS impact on net cover (Fig. 3a).

Fig. 3 COTS density ($2+$ yr COTS·ha⁻¹) encountered by COTS control program cull divers, that model results suggest keeps coral in equilibrium for (a) fast-growing coral for a number of model sensitivity runs (Table 2) and compared with the outbreak threshold (10 COTS ha⁻¹) defined by Keesing and Lucas (1992) for coral cover of 20% to 50% and (b) slow-growing coral stabilising at the specified levels when fast-growing coral is held constant at 20% and 50% coral cover. See Table 2 for summary of methods used



The *Coralf* base growth rate is much larger than that of *Coralm*. Hence, although both groups are modelled similarly, changes in the density-dependent growth rate of the fast-growing corals is better able to offset starfish consumption. This contrasts with the slow-growing corals where their slower growth is easily dominated by starfish

consumption across its range of abundance. Additionally, as the abundance of preferred fast-growing corals declines and/or the abundance of slow-growing corals increases, starfish increasingly supplement their diet with slow-growing corals. This is such that the starfish population that equilibrates slow-growing coral growth is monotonically

and inversely related to its abundance where the average slope of the relationship is determined by the abundance of fast-growing corals. Hence fewer fast-growing corals lead to flatter curves (Fig. 3b)—fewer COTS will equilibrate slow-growing coral growth.

The number of COTS is shown in units of both numbers of large age 2+ yr COTS·ha⁻¹ as well as the total number of 1-yr and 2+ yr COTS·ha⁻¹ (Table 4). The conversions between different field observations (assuming the true underlying abundance is known) highlights the scale of the problem because the actual numbers can be more than an order of magnitude larger and include a lot of small COTS that will remain undetected during a single culling operation. In addition, assessments of COTS population structure are confounded by movement of COTS and variable individual somatic growth rates (and sex ratios), but these factors are beyond the scope of the current analysis. The 2+ yr and total COTS densities are converted to CPUE rates (Table 4). The results of a number of sensitivities using alternative parameter settings are also shown alongside.

CPUE-COTS density relationship

The catchability parameter q of the CPUE-COTS relationships was estimated with good precision (Table 3). This only applied to hyper-stability values h between 0.5 and 1.0; at values of h lower than 0.5, the estimated values of q were impossible (> 1.0). The likelihoods computed for each alternative model measure the probability of the data given the parameter estimates, and therefore comparisons of likelihoods can be used to select the model which fits the data best statistically. The best model fit and hence relationship is described by $h = 0.5$ (denoted with * in Table 3). The CPUE trajectory using the best-fit value is illustrated in Fig. 4.

Comparing model results and field data

We use as the reference CPUE the measure that is most directly comparable to field CPUE measures (Table 4). This estimate accounts for the size distribution of COTS removed in the field using the hyper-stability relationship (Eq. 9) and accounting for differing detectability of 1-yr and 2+ yr COTS. These measures are used to produce a plot of the COTS CPUE (comparable to field CPUE estimates) that restricts the fast-growing coral cover at a zero-growth rate level for coral cover across a range of levels as shown in Fig. 5 (with values shown in Table 4).

For coral cover in the range 20–40%, and considering the sensitivity analyses, these results suggest that the COTS CPUE should be below approximately 0.04–0.06 COTS/min to maintain existing coral cover and promote recovery.

Table 3 Estimates of q at different fixed values of h to different values, including the asymptotic standard errors (SD), coefficients of variation (CV) and likelihood values (calculated as the sum of squares)

| h | q | SD | CV | Likelihood |
|-----|-------|-------|-------|------------|
| 0.5 | 0.669 | 0.011 | 0.016 | 322.87* |
| 0.6 | 0.374 | 0.006 | 0.016 | 346.35 |
| 0.7 | 0.206 | 0.003 | 0.016 | 383.15 |
| 0.8 | 0.112 | 0.002 | 0.016 | 428.26 |
| 0.9 | 0.061 | 0.001 | 0.016 | 477.61 |
| 1.0 | 0.033 | 0.001 | 0.017 | 528.13 |

*Denotes the best relationship

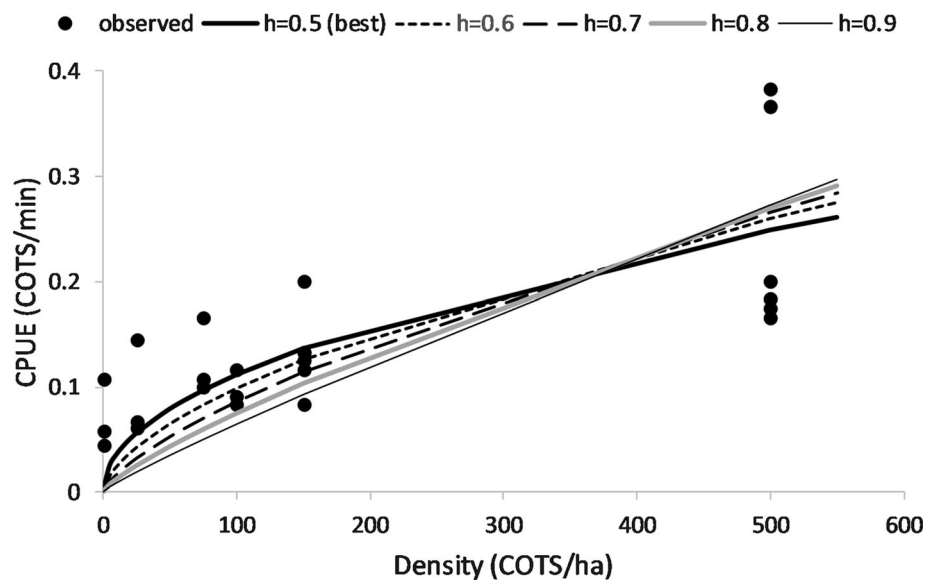
Figure 5 also shows the average coral cover from all 87 reefs that formed part of the COTS management program in 2012–2014 was 35% (Online Resource 1: Table S6), within the range described above.

To illustrate the rate at which coral cover can be expected to vary under different scenarios, we plotted the percentage change (per year) in fast-growing coral cover for CPUE (COTS/min) rates and coral cover percentages (Fig. 6). This shows that if culling continues until the CPUE is reduced below the threshold values, what the expected rate of coral recovery might be, compared with expected declines in coral cover when CPUE (and hence the underlying numbers of COTS grazing on coral) is above the threshold value (Fig. 6). The plots show the relative gradients where rapid changes in coral cover can be expected. This highlights where improvements in coral cover are likely to be greatest when reducing COTS numbers—for example, at low coral cover, the same change in CPUE has a bigger impact than at higher coral cover, and coral cover declines more quickly as CPUE is increased than it is able to recover in response to decreases in CPUE (Fig. 6).

Sensitivity analyses and validation of results

The two alternative methods used to convert between different density estimates yielded similar results. In addition, a number of sensitivity tests were run to evaluate the effect on results of alternative parameter settings given there is considerable uncertainty regarding bias correction factors for sightability and detectability. Sensitivity to the form of the CPUE-density relationship could be tested in the future as more cross-calibration data become available. The list of key sensitivity scenarios is shown in Table 2 and results compared in Fig. 5. In addition, we tested the sensitivity of results when assuming both a faster ($r^f = 0.6$) and slower ($r^f = 0.4$) fast-growing coral growth rate (compared with

Fig. 4 Catch per unit effort (COTS/min) against COTS density (COTS·ha⁻¹) shown when using the best-fit hyperstability parameter of $h = 0.5$, compared with alternative values of h (see also Table 3)



the base-case value of $r^f = 0.5$) and we found that model results were fairly robust to changes in this parameter, with only a slight increase and decrease, respectively, evident in the CPUE versus coral cover relationship (Online resource 1: Fig. S1).

Analysis of the COTS control program data from all reefs culled over 2012–2014 supports that COTS were outbreaking in high numbers across a number of reefs, with many very high (> 0.5 COTS/min) CPUE records, as well as evidence of the control program successfully reducing CPUE below the threshold levels of around 0.05 COTS/min derived in these analyses (Online resource 1: Fig. S2).

Discussion

This study highlights how existing data sets can be used in combination with quantitative modelling approaches to derive population thresholds for use in pest management and ecosystem-based management applications. For fast-growing coral, there is a point at which the balance between the rate of growth of coral and the removal through grazing by COTS moves from net growth to net decline. The model steady-state analysis suggests that if coral cover is higher, then the same number of COTS will have less impact on the system than for lower levels of coral cover (Fig. 3). Hence, at higher coral cover levels, net growth in coral cover remains constant when there are more COTS present than is the case at lower coral cover levels: for example, if the coral cover is 80%, then the model suggests that as many as 14 COTS·ha⁻¹ (2+ yr COTS) could be detectable on a reef without causing a further decline in the coral cover, compared with 4 COTS·ha⁻¹ when the coral cover is 20%. This provides a

basis for enabling management programs to make operational estimates of COTS CPUE target levels at reefs with a range of coral cover. However, at high levels of coral cover it may still be desirable to reduce COTS densities well below the cover-specific outbreak level thresholds, particularly where this may be at or above threshold levels of fertilisation success or zygote production (Rogers et al. 2017). This may have the benefit of inhibiting the formation of a secondary outbreak and would need to be a factor in prioritization and triage around a regional COTS management program, as highlighted by network modelling of COTS metapopulation dynamics (Hock et al. 2016). Although it is challenging to manage outbreaks, ongoing research to improve efforts to manage COTS is important because other major causes of coral loss, such as climate-induced bleaching, are less amenable to direct interventions (Pratchett et al. 2017).

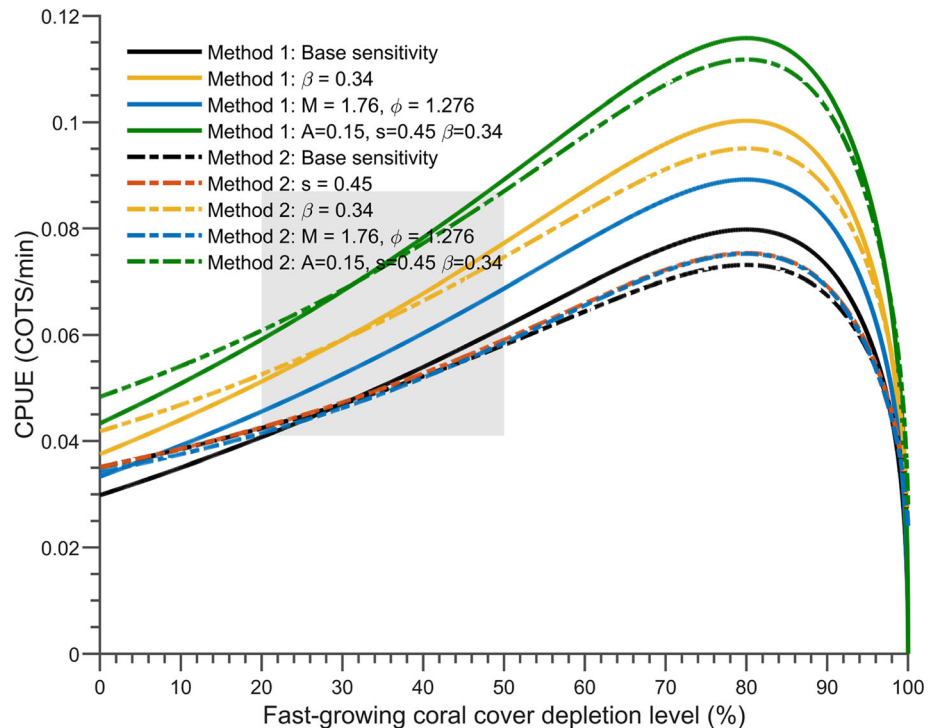
In order to validate results using empirical information, we compared our model results with the outbreak threshold (10 COTS·ha⁻¹) defined by Keesing and Lucas (1992) which was derived independently based on data for reefs having a coral cover ranging between 20% and 50% (Fig. 3). This cover also aligns closely with the average coral cover recorded on reefs that were being managed by the COTS control program from 2012 to 2014. Our model results compare well with these empirical estimates, suggesting outbreak thresholds are in the range 3–8 adult COTS·ha⁻¹ (Fig. 3). More recently, MacNeil et al. (2016) inter-calibrated multiple data sources and estimated that COTS densities in the Cairns sector of the GBR averaged 44 adults COTS·ha⁻¹ in 2014. They estimated densities in excess of 62 COTS·ha⁻¹ in northerly (outbreaking) reefs compared with densities below 12 COTS·ha⁻¹ for southerly reefs, which they noted were mostly non-outbreaking,

Table 4 Summary of the number of COTS and conversions to field observations of densities and corresponding CPUE that keep fast-growing coral in equilibrium at different coral cover levels as shown in Fig. 3

| | Total | >15 cm | <15 cm | MANTA tow sampling (MC) | SCUBA transect sampling (SC) | Method 1 | Method 1 | Method 1 | Method 2 | Sens 2 | Sens 3 | Sens 4 | Sens 5 |
|---------------------------|-------------------------|-------------------------|-------------------------|---|--|--|------------------|---|---|--------------------------------|--------------------------------|--------------------------------|---------------------------------------|
| | | | | | | | | | | | | | |
| Coral Cover (fastgrowing) | Actual Total no.COTS/ha | Actual Total 2+ COTS/ha | Actual 1-yr-old COTS/ha | MANTA Ecological threshold COTS/ha seen (> 15 cm) | SCUBA Ecological threshold COTS/ha (> 15 cm) | Cull Program Ecological threshold TOTAL COTS seen/ha | CPUE 2+ COTS/min | Method 1 (convert actual no. to SC then cull no.) | Method 2 (convert MC to SC then cull no.) | Sens 2 (greater sightability) | Sens 3 (greater detectability) | Sens 4 (model M) | Sens 5 (manta area, sight and detect) |
| | | | | | | | | Alternative cull CPUE COTS/min | Alternative cull CPUE COTS/min | Alternative cull CPUE COTS/min | Alternative cull CPUE COTS/min | Alternative cull CPUE COTS/min | Alternative cull CPUE COTS/min |
| 0 | 30.0 | 2.3 | 27.7 | 0.10 | 1.90 | 7.16 | 0.02 | 0.030 | 0.035 | 0.028 | 0.022 | 0.033 | 0.051 |
| 0.05 | 35.3 | 2.7 | 32.6 | 0.12 | 2.24 | 8.43 | 0.02 | 0.032 | 0.037 | 0.028 | 0.023 | 0.036 | 0.056 |
| 0.1 | 41.3 | 3.2 | 38.1 | 0.14 | 2.62 | 9.86 | 0.02 | 0.035 | 0.038 | 0.028 | 0.024 | 0.039 | 0.060 |
| 0.15 | 48.2 | 3.7 | 44.4 | 0.16 | 3.05 | 11.49 | 0.02 | 0.038 | 0.040 | 0.028 | 0.025 | 0.042 | 0.065 |
| 0.2 | 55.9 | 4.3 | 51.6 | 0.19 | 3.54 | 13.34 | 0.02 | 0.041 | 0.042 | 0.028 | 0.027 | 0.046 | 0.070 |
| 0.25 | 64.7 | 5.0 | 59.7 | 0.22 | 4.10 | 15.43 | 0.02 | 0.044 | 0.045 | 0.028 | 0.028 | 0.049 | 0.075 |
| 0.3 | 74.5 | 5.8 | 68.7 | 0.25 | 4.72 | 17.78 | 0.02 | 0.047 | 0.047 | 0.028 | 0.029 | 0.053 | 0.081 |
| 0.35 | 85.6 | 6.6 | 78.9 | 0.29 | 5.42 | 20.42 | 0.03 | 0.050 | 0.050 | 0.028 | 0.031 | 0.056 | 0.087 |
| 0.4 | 98.0 | 7.6 | 90.4 | 0.33 | 6.21 | 23.39 | 0.03 | 0.054 | 0.052 | 0.029 | 0.032 | 0.060 | 0.093 |
| 0.45 | 111.9 | 8.7 | 103.2 | 0.38 | 7.09 | 26.71 | 0.03 | 0.058 | 0.055 | 0.029 | 0.034 | 0.064 | 0.099 |
| 0.5 | 127.3 | 9.8 | 117.5 | 0.43 | 8.07 | 30.39 | 0.03 | 0.061 | 0.058 | 0.029 | 0.036 | 0.069 | 0.106 |
| 0.55 | 144.1 | 11.1 | 132.9 | 0.48 | 9.13 | 34.39 | 0.03 | 0.065 | 0.061 | 0.030 | 0.038 | 0.073 | 0.112 |
| 0.6 | 161.8 | 12.5 | 149.3 | 0.54 | 10.26 | 38.62 | 0.04 | 0.069 | 0.064 | 0.031 | 0.040 | 0.077 | 0.119 |
| 0.65 | 179.8 | 13.9 | 165.9 | 0.60 | 11.39 | 42.91 | 0.04 | 0.073 | 0.067 | 0.031 | 0.042 | 0.082 | 0.126 |
| 0.7 | 196.3 | 15.2 | 181.1 | 0.66 | 12.44 | 46.86 | 0.04 | 0.076 | 0.070 | 0.032 | 0.044 | 0.085 | 0.131 |
| 0.75 | 209.2 | 16.2 | 193.0 | 0.70 | 13.26 | 49.92 | 0.04 | 0.079 | 0.072 | 0.033 | 0.045 | 0.088 | 0.135 |
| 0.8 | 214.5 | 16.6 | 197.9 | 0.72 | 13.60 | 51.20 | 0.04 | 0.080 | 0.073 | 0.033 | 0.045 | 0.089 | 0.137 |
| 0.85 | 207.1 | 16.0 | 191.0 | 0.70 | 13.12 | 49.42 | 0.04 | 0.078 | 0.072 | 0.033 | 0.045 | 0.088 | 0.135 |
| 0.9 | 179.3 | 13.9 | 165.4 | 0.60 | 11.36 | 42.79 | 0.04 | 0.073 | 0.067 | 0.031 | 0.042 | 0.082 | 0.125 |
| 0.95 | 121.8 | 9.4 | 112.4 | 0.41 | 7.72 | 29.07 | 0.03 | 0.060 | 0.057 | 0.029 | 0.035 | 0.067 | 0.103 |
| 1 | 0.0 | 0.0 | 0.0 | 0.00 | 0.00 | 0.00 | 0.00 | 0.001 | 0.024 | 0.028 | 0.016 | 0.001 | 0.001 |

The number of COTS is shown in units of manta tow and SCUBA (numbers of large age 2+ COTS ha⁻¹), as well as the total number of 1 and 2+ COTS ha⁻¹ that are encountered by COTS control program divers during culling operations. The COTS densities are converted to CPUE rates, shown as the number per minute, in units that have been matched as closely as possible to that recorded in field surveys. Alternative values are shown when applying sensitivities as described in Table 2

Fig. 5 Model-derived relationship between CPUE (COTS/min) and equilibrium fast-growing coral cover proportion. The average observed coral cover recorded in the COTS control program 2012–2014 database is shown as part of a shaded box that includes one standard deviation on either side and which also encompasses the range of likely CPUE rates that correspond to the ecological threshold. The vertical axis units are those which correspond most closely to the units of the CPUE measures recorded in the field, namely mostly age 2+ yr COTS individuals plus a smaller percentage (the detectability) of the age 1+ COTS removed per minute (see text for details)



which is consistent with the COTS densities estimated in this study (Table 4). In some instances, outbreak densities can be exceedingly high ($> 1000 \text{ COTS} \cdot \text{ha}^{-1}$) throughout the Indo-West Pacific reefs (Pratchett et al. 2017), for example a survey of a recent outbreak on a Republic of Maldives reef observed an average density of $362 \text{ COTS} \cdot \text{ha}^{-1}$ (Saponari et al. 2018).

The dome shape of the curve in Fig. 3A is similar to a sustainable yield curve as classically used in fisheries management, and is shifted to the right because of the high growth rate of fast-growing coral (*Coralf*). We modelled coral growth using a logistic type growth curve (Schaefer model) so the turnover rate is fastest at intermediate population levels (in this case intermediate coral cover) which is why the largest number of COTS can be sustained at those levels (i.e. we calculated the equilibrium balance between the number of COTS and coral cover so the COTS are eating surplus production at those levels, but not dropping the total coral cover further). The sensitivity to alternative assumed coral growth rates can be readily investigated.

The pattern above contrasts with the shape estimated for slow-growing coral (*Coralm*), because the latter has a much slower rate of growth and hence the production curve is expected to take a different shape. But this is also complicated further by the interaction between the two coral species and COTS switching between them. The COTS are assumed to switch to feeding on slow-growing corals once the fast-growing corals become heavily

depleted (Moran 1986). At high *Coralm* levels, there might be less *Coralm* and so COTS may focus less on them, but when there are lots of COTS and *Coralf* is held constant, they will focus on *Coralm*, which complicates the overall dynamics. Figure 3B suggests that if the fast-growing coral are more heavily depleted, the COTS will increasingly supplement on slow-growing coral and hence relatively fewer COTS will result in a decline of the slow-growing coral below a pre-specified depletion level. Figure 3B also shows that holding *Coralf* at a higher level means more COTS can be supported on the reef, noting the result shows the number of COTS in equilibrium with the joint *Coralf* and *Coralm* biomass levels which are related. Sensitivity to alternative growth rates of slow-growing coral can similarly be readily investigated.

Alternative growth scenarios for both fast and slow-growing corals might include varying rates of impacts such as cyclone damage and coral bleaching (Condie et al. 2018). In the context of coral reef resilience, it is significant to note that the fast-growing coral species preferred by COTS are also broadly speaking those most susceptible to bleaching (Keesing et al. 2019). Given limited data, our model used a simple categorisation of coral into fast-growing and slow-growing groups, but future work could advance our efforts through better representation of coral species composition and spatial distribution. Indeed, previous work has demonstrated that although they show a preference for acroporid and pocilloporid corals (Keesing et al. 2019), there are many factors (e.g. nutritional content,

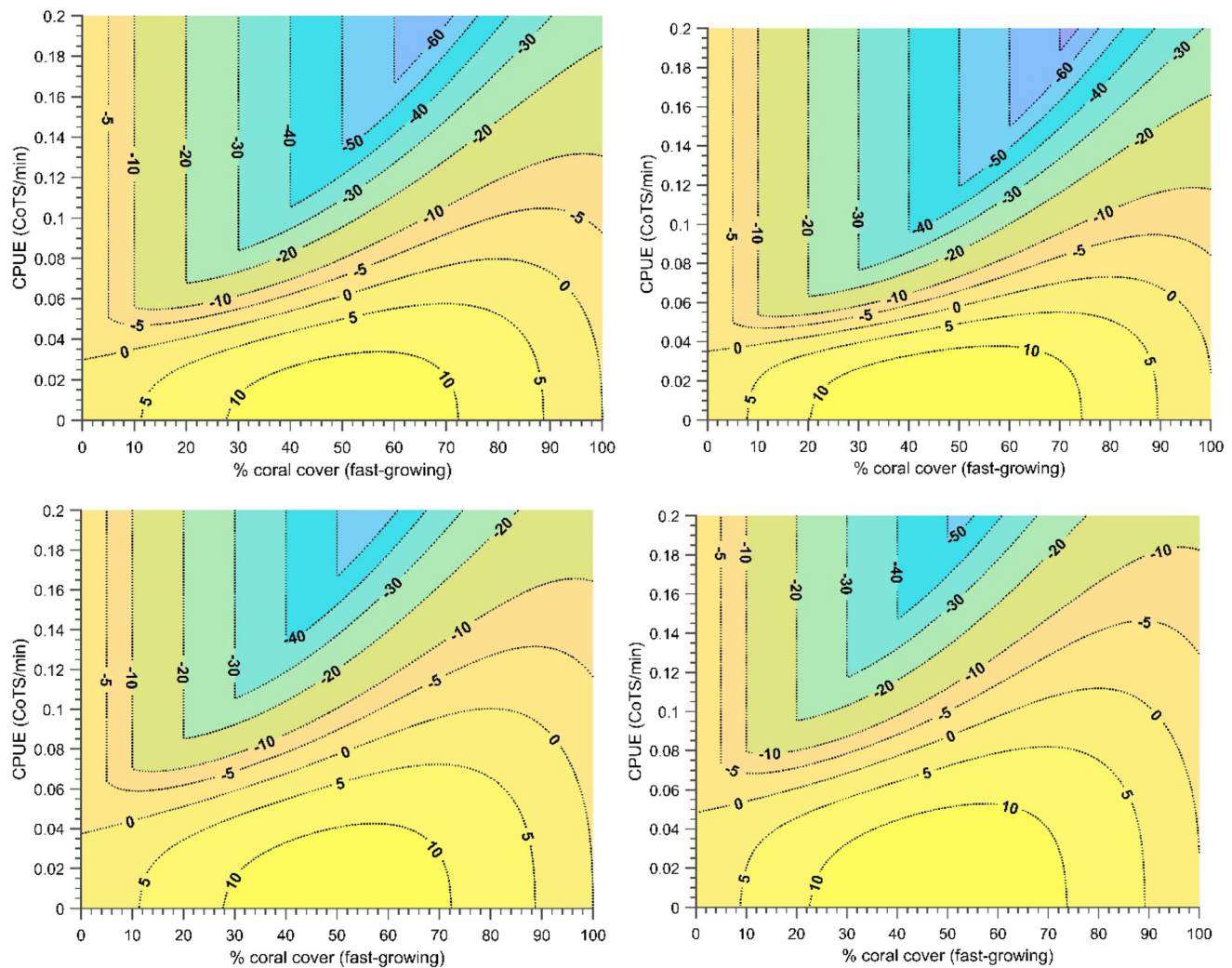


Fig. 6 Model-derived expected percentage change (per year) in fast-growing coral cover for CPUE (COTS/min) rates and coral cover percentages as shown. Increases or decreases in coral cover are due to the differences between COTS grazing versus coral growth rates, where the zero isocline represents the equilibrium when COTS

densities and coral cover are balanced and coral cover thus does not decrease below the corresponding COTS densities. Selected examples are shown for alternative parameterisations as detailed in Table 2 and as follows from top left to bottom right: Method1, Method2, Sensitivity 3 and Sensitivity 5

coral defenses, coral distribution and availability) that influence COTS feeding preferences (Pratchett et al. 2014, Keesing et al. 2019) and hence more explicit representation of the coral composition could be used to refine model results.

Our study used both field observations and model predictions to estimate detectability of the 1-yr COTS (those we classified as younger than 2 yrs) by cull divers at 19%, with a sensitivity analysis suggesting that the relative proportion (or detectability) of small COTS may have increased over time (Table 2; Table S5). The likely low detectability of smaller COTS highlights the need for frequent revisits by field control teams to effectively reduce the numbers of COTS. We used results from a mark-recapture type field study (MacNeil et al. 2016) that found

the detectability of adult COTS (equivalent to 2+ yr COTS described in this study) was high at 82% [with 95% uncertainty interval 77–87%]. No comparison is available for the 1-yr detectability as smaller COTS were not observed in the MacNeil et al. (2016) study, but these authors note that detectability declines substantially with decreasing size, and other factors also influence detectability, namely site and time of day. Indeed, a study of COTS around Moorea, French Polynesia, estimated 27% higher COTS densities at night compared to during the day, underscoring the need to account for detection bias in surveys and control programs (Kayal et al. 2017).

Through statistically fitting to data collected at Lizard Island by Fisk and Power (1999) we developed a CPUE-COTS density equation that can be used to convert between

estimates of COTS density and field observations of the numbers of COTS monitored by manta tow methods, observed by SCUBA divers on transects or culled per unit time (Fig. 1). CPUE data can provide an index of the relative abundance of COTS in the field, but relating this directly to the underlying abundance or density of the population is confounded by the fact that this relationship is seldom linear, and factors such as handling time mean that a hyper-stable relationship (i.e. the CPUE values start converging to some asymptotic value at high COTS densities) is more likely (Fig. 4). Although based on relatively few data, the hyper-stable CPUE-COTS density relationship we derived is similar to that estimated by MacNeil et al. (2016) using a different data set. The hyper-stable formulation captures that when COTS density is reduced, CPUE is higher than predicted from a linear relationship as might be the case, for example, if COTS are aggregated on remaining live coral patches. Explicit representation of more complex relationships such as due to the distribution and composition of coral communities is beyond the scope of this study, but would be worthwhile investigating further (see also Pratchett et al. 2017).

We computed CPUE statistics that took into account the detectability of large and small-sized COTS in the field, and hence in units that are most directly comparable to field CPUE measures (i.e. it accounts for the size distribution of COTS removed in the field). The threshold COTS CPUE values are intended as reference levels describing the levels, for coral cover across a range of levels as shown in Fig. 5, below which COTS populations should be reduced in order to prevent further declines in the fast-growing coral cover. For coral cover in the range 20–40%, these preliminary results suggest that the COTS CPUE should be maintained below approximately 0.04–0.07 COTS/min to keep the coral cover stable at its current level. The average (\pm STD) coral cover at the time of these analyses was 35% (\pm 17%) with range 3–88% (Online Resource 1: Table S6). This suggests that on average, CPUE target rates should be less than 0.05 COTS·min⁻¹ (1 COTS per 20 min) and for low coral cover, CPUE target rates should be lower, down to around 0.04 COTS·min⁻¹ (1 COTS per 25 min) (Table 4).

The finding from this study that the sub-outbreak threshold density of COTS (and hence the CPUE) is reduced at lower coral cover, provided scientific support for the management approach applied at the time which recommended that efforts to cull COTS focus on achieving a larger reduction in CPUE when coral cover is below, rather than above 40%. The findings from this study have also underpinned the choice of threshold level to guide field management efforts, namely the following are adopted as management targets in the expanded COTS control program (Fletcher et al. 2020):

- 0.04 COTS·min⁻¹ where coral cover is < 40%
- 0.08 COTS·min⁻¹ where coral cover is > 40%.

Fletcher et al. (2020) also demonstrate the capacity of the program to achieve these ecologically-informed management targets, and provide recommendations for future refinement.

Our results were reasonably robust across a range of sensitivity tests. For example, to maintain coral cover at 35%, the CPUE estimated values ranged from 0.03 to 0.08 (Fig. 5). The higher estimate of 0.08 COTS·min⁻¹ (ca. 3 COTS per 40 min) derived from Sensitivity 5 and is not surprising because this scenario assumed a greater proportion (34% versus the base value of 19%) of 1-yr COTS are successfully culled. Hence the CPUE threshold is expected to be higher as it corresponds to an improved detection ability relative to the base scenario. This also underscores the disproportionate negative impact on COTS (and conversely positive impact on coral recovery and success of a culling program) of being able to locate and cull younger COTS.

Some historical data, such as Fisk and Power (1999) that we used to fit the hyper-stable CPUE-COTS relationship, are not entirely applicable to the current situation. This is because they used a different, less efficient, removal method compared to those used at present, as well as the limited spatial coverage of the removals. As a result, we also tested sensitivity of our results by drawing on the more recent study of MacNeil et al. (2016). Fisk and Power (1999) presented simultaneous quantification of both removals (CPUE) and density of COTS (including small animals) in the water (N), and these data were therefore more suited for the current analyses than the COTS management control data. Future data collection efforts should be expended to collect data that can better inform the efficiency of control efforts: this requires repeated surveys measuring different COTS densities in situ followed by CPUE from removals. Surveys and culling operations need to include sampling of small COTS (< 15 cm) and should ideally test for sampling differences between more and less experienced divers. Simultaneous manta tow and SCUBA transect sampling will also be helpful in further refining conversion factors between different methods. Finally, simultaneous detailed sampling of coral cover and spatial distribution will improve understanding of the dynamics of COTS and coral populations with the goal of improving decision-making as part of the overall COTS management strategy on the GBR (Fletcher et al. 2020). Ongoing technological improvements in sampling methods, such as a digital droplet PCR method to detect environmental DNA (eDNA), also show considerable promise in supplementing traditional monitoring methods in the future (Uthicke et al. 2018). Improved monitoring of coral abundance, species

composition and recovery rates alongside COTS control data will also lead to ongoing improvements in assessing and managing COTS outbreaks.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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