Coral loss caused by an outbreak of Crown-of-thorns sea star (Acanthaster planci) at a shallow reef in Dauin, Philippines

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Abstract

Coral reefs are increasingly under threat and one of the most severe local threats is outbreaks of the corallivorous Crown of Thorns starfish (COTS). One way of mitigating COTS outbreaks is to cull them by injecting vinegar, however it is very labour intensive. This study focuses on the risk of COTS predation by measuring changes in coral cover and COTS present on 40 coral colonies at risk of COTS predation, mostly *Acropora* species, on a small reef in masaplod Sur MPA, Dauin, Negros Oriental, Philippines.

Coral loss rates averaged 333.8 cm^2 day^{-1} colony^{-1} before the first cull took place, then 76.76 cm^2 day^{-1} colony^{-1} when culls were done weekly. In 45 days, coral loss amounted to 24.57 m^2 on 38 colonies, representing 33.9% of the total coral area where most of the loss occurred in the first 17 days when no culls were done. In total, 712 COTS (650 of which found on *Acropora spp.*) were recorded on the 40 (38 *Acropora spp.*) monitored corals. The highest number of COTS found on one day was 82 (75) and daily counts decreased significantly in the period of weekly culling. Visible COTS measured 16.3 - 34.7 cm in diameter with an average of 24.7 cm. COTS were commonly found aggregating, with average count being 4.05 (3.95) when COTS are present. 74.3% of COTS found on *Acropora* colonies would be found underneath the coral table or in crevices (cryptic), and COTS were found to be more cryptic when culls are done weekly. Predation rates by individual COTS were estimated to be 126.1 cm^2 coral day^{-1} COTS^{-1} pre-culling but significantly higher after the first cull at 223.1 cm^2 coral day^{-1} COTS^{-1}. However, when coral loss occurs, loss rates were not found to differ whether culls are ongoing or not. Individual feeding rates do not appear to change significantly depending on the number of COTS on the same coral. Feeding rates are similar to what is previously recorded in earlier studies. The COTS population in this outbreak is likely to be young and have most likely been feeding on corals for 3 years. Methods deployed in this project are easy to deploy in less funded marine conservation projects but there are accuracy considerations with this model and corrections are needed. Culls by vinegar injection are effective in decreasing overall COTS predation but despite weekly culls coral loss still occurs. Despite the laborious culling, it is likely the most suitable action when an outbreak is ongoing as it decreases coral loss and prevents COTS aggregation and subsequent reproduction, protecting neighbouring reefs from new outbreaks.

Keywords

Popular summary

Coral reefs are increasingly threatened by human-induced global changes. The crown-of-thorns sea star (COTS) is a big coral-eating sea star that tends to explode in numbers within a small area, which is happening more often due to more nutrients going into the sea in coastal areas. Management of COTS outbreaks as they are known are usually done by vinegar injection, reducing numbers quickly locally however it is labour intensive. COTS react to chemical stimuli from predators and other COTS feeding, but how do feeding rates, coral loss rates and COTS behaviour change in an outbreak where culls are ongoing? This project studies this by tracking COTS numbers, position, live coral and changes over time on 40 coral colonies in a reef with an active outbreak in Dauin, Philippines. In 45 days, COTS were responsible for a 33.9% loss in coral cover in this period, of which 24.0% in the first 17 days before the first cull. A total of 712 COTS were found, mostly underneath corals. Culling was proven effective in decreasing numbers found up to a week after culls, and COTS were more likely to hide after first cull. Coral loss due to COTS does not differ after first cull and COTS aggregating does not lead to higher predation rates but COTS predation rates were found to increase slightly after first cull. Feeding rates are similar to previously recorded in earlier studies. The COTS population in this outbreak has likely been feeding on corals for 3 years. Methods deployed in this project are easy to deploy in less funded marine conservation projects. Culls by vinegar injection are effective in decreasing but do not stop coral loss entirely, it is likely the most suitable action when an outbreak is ongoing as it decreases coral loss and prevents COTS aggregation and subsequent reproduction, protecting neighbouring reefs from new outbreaks.

Ethical and social aspects

This project has included the deliberate killing of animals usually considered pests in what has become a common practice in population control of COTS. The culls result in death for the injected COTS usually within 24 hours. Sea stars are not considered to have an advanced nervous system but there is an instant flight response to injections which undoubtedly is a result of increased stress in the animal. The injection substance (vinegar) is safe for surrounding marine life and the removal of COTS vastly outweighs the reef degradation such high population densities cause without intervention. In fact, the initial period of no intervention has caused a period of significant degradation, but due to the efforts of this project more focus has been put on the outbreak and the damages caused than if this project had not gone ahead. The cull response has therefore been more thorough with weekly culls still ongoing months after the project end date. While the COTS outbreak remains, the constant cull pressure results in increased conservation of the reef, helping residents and the community dependent of the food and tourism the reef provides. As this study expands our knowledge of COTS behaviour and response to culls, management of COTS outbreaks will be better informed and acting less on assumptions or anecdotal evidence, leading to more effective conservation efforts.

Contents

Introduction

Coral reefs are important ecosystems that provide a range of ecosystem services and contain large diversity of organisms (e.g. Rasher et al, 2013). Increasing anthropogenic activities such as fishing (Hutchings, 1986; Sweatman, 2008), increased coastal nutrient loading (Birkeland, 1982; Brodie, 2005; Uthicke et al, 2015), coastal development activities (Hughes et al, 2003; Baird et al, 2013) and factors contributing to climate change (Uthicke et al, 2015) all contribute to a heavy decline in coral cover. As coral reefs decline, there is a catastrophic loss of associated species, specialised in living in coral reefs. Corallivorous sea stars are notable predators and can cause large disruptions and degradation to coral reefs, and of particular interest is the Crown-of-thorns sea star (COTS; Acanthaster planci; Chesher, 1969; Baird et al, 2013).

A. planci is a large sea star fitted with defensive spikes that deliver a potent toxin (Komori, 1997) and is prone to large local population increases, or outbreaks, that severely degrade coral reefs (Chesher, 1969, Uthicke et al, 2009; Pratchett et al, 2009). Predation by COTS causes catastrophic coral loss which leaves the coral skeleton exposed and this is rapidly colonised by algae (Glynn, 1973; Hutchings, 1986; Kenchington and Kelleher, 1992). Algal colonisation begins when corals are degraded to the point the calcareous skeleton is exposed, after which algal colonisation typically occurs within 24 hours (Chesher, 1969; Belk and Belk, 1975). Healthy reefs with low levels of degradation still maintain a diverse community composition that will graze and ward off competitive macroalgae (McCook et al, 2001; Rasher et al, 2013), which grants healthy reefs an inherent resilience. Predation on COTS larvae, primarily by fish, results in high juvenile mortality (Keesing et al, 2018; Cowan et al, 2020). Higher fishing pressure however correlates with an increased abundance of COTS, likely an effect of the loss of fish predating on COTS larvae (Sweatman, 1995; Sweatman, 2008; Keesing et al, 2018; Westcott et al, 2020). Furthermore, with increased coral reef degradation comes greater susceptibility towards shifting to a macroalgal-dominated system and this shift is hard to reverse when the diversity of grazers is lost (Scheffer et al, 2001; Briggs et al, 2018), with affected reefs having very low densities of coral colonies >20 cm diameter for decades post-outbreak (Endean et al, 1988). Coral success is severely reduced with macroalgal dominance due competition for space and substrate and subsequently lack of available substrate for coral recruitment (McCook et al, 2001), which affects reproduction negatively (Monteil et al, 2020).

The reported number of COTS outbreaks have been found to be increasing in later years (Baird et al, 2013; Uthicke et al, 2015). The increased success in recruitment and increased frequency of outbreaks have been linked to increased terrestrial runoff in coastal areas promoting higher algal growth, increasing the primary food source for juvenile COTS (Birkeland, 1982). Increased sea surface temperatures (SST) resulting from global warming also contributes to the growth of juvenile COTS although food is still the primary growth factor (Uthicke et al, 2015). Juvenile COTS are cryptic and feed on algae or biofilm before emerging, between 4 months up to 6.5 years of age, and starting to feed on corals.They usually feed nocturnally, making them 'a hidden army' in coral reefs (Zann et al, 1987; Deaker et al, 2020a; 2020b). Once COTS start feeding on corals, there is a clear preference for certain coral morphologies where they often aggregate to feed. COTS are more likely to predate on tabulate or branching corals (Keesing and Lucas 1992; De'ath and Moran 1998b). The most commonly predated genus is Acropora, with many species growing tabulate or branch-forming colonies, while massive Porites and Montipora corals often being common secondary preferences (Chesher et al, 1969; Baird et al, 2013). While COTS can move significant distances, large tabulate corals provide ample cover and COTS can often be found hiding underneath (Chesher et al, 1969; Zann et al, 1987; Keesing, 2015). COTS movement has been measured to average 2.8m in low COTS density/high coral density and 10.3 m d-1 in high COTS density/low coral density (Keesing & Lucas, 1992). Other studies report up to 250 m per week (Chesher, 1969). COTS are usually considered to be nocturnal predators (Chesher, 1969; Keesing, 1995), but feeding time of day is primarily determined

by size with COTS <20cm diameter mostly being nocturnal feeders and >40cm diameter diurnal (Zann et al, 1987; Keesing, 1995). Generally however, COTS appear to be negatively phototaxic and will attempt to hide in a shaded area (Zann et al, 1987; Keesing, 1990). COTS appear to aggregate due to feeding availability and activity (Dana et al, 1972; Ormond et al, 1973) and when they aggregate they appear to show no light-avoiding behaviour but no difference was seen in the proportion of cryptic COTS (Keesing, 1995).

Because of the rapid degradation of coral reefs due to COTS outbreaks, proper management of COTS populations is a key issue. Management of coral reefs is a multi-faceted issue combining preventative actions, such as ensuring good ecological status and water quality and handling more acute events like COTS outbreaks (Brodie et al, 2005; Westcott et al, 2020). COTS have some natural predators like the Triton's Trumpet Sea snail (*Charonia tritonis*) but it is not a specialist predator of COTS and occurs normally in low abundances, and has as such little effect on COTS populations (Chesher, 1969). It is therefore important to conduct population controls (culls) to limit the extent of coral loss in the affected area. Culls are usually done by injection of COTS with substances lethal to the COTS individual but little-to-no effect on surrounding biota. Effective injection substances include chemicals like copper sulphate, sodium bisulphate and bile salts (Johnson et al, 1990; Rivera-Posada et al, 2014). However, a cheaper and more accessible option is household vinegar. Household vinegar injections have no short or long-term effects on coral cover, disease prevalence and fish health (Yamamoto et al, 2013; Boström-Einarsson et al, 2018). Having access to cheap and effective methods to reduce COTS predation is especially important for management in less funded MPAs found in the coral triangle, where management would otherwise be costly (Kenchington and Kelleher, 1992; Baird et al, 2013).

Another aspect of managing COTS outbreak is knowing the impact on coral cover and the entire local ecosystem. It is also important to know the impact and efficiency of actions taken, however little research has been done on coral loss rates due to COTS outbreaks and what, if any impact culling has on overall COTS predation rates. While there have been studies on individual predation rates (Keesing & Lucas, 1992) and several reports of the extent of outbreak degradation (Chesher et al, 1969; Baird et al, 2013; Westcott et al, 2020), none of these studies have gone into detail about what effects culls have on predation rates or COTS behaviour. Likewise, culls have been continuously questioned in their efficiency in stopping COTS outbreaks due to their cryptic nature where divers may miss a substantial number of hiding individuals during culls (Johnson et al, 1990; Kenchington and Kelleher, 1992).

This study aims to fill that knowledge gap by investigating change in coral cover, estimating individual COTS predation rates by measuring change rates pre- and post-cull in an affected reef. The literature on this matter is limited but COTS, like other asteroids, rely heavily on chemical stimuli that affect behaviour (Hall et al, 2017). Additionally, a culling trial done outside and downstream of the study MPA was observed to heavily decrease COTS densities in the area beyond the number of injected individuals. If injected and decomposing COTS would be sensed as imminent danger for other COTS similar to the predator avoidance behaviour witnessed from the presence of C. tritonis (Chesher et al, 1969; Hall et al, 2017). This would in turn result in less time spent foraging and moving and more time spent cryptic, thus reducing metabolic demand and decreased coral predation rate. The working hypotheses are that

- culls which cause a quick decrease in COTS density will result in lower individual predation rate and a significant decrease in overall coral loss, and
- more COTS will be displaying evasive and predator avoidance behaviour by hiding under corals and in crevices rather than being on corals or otherwise in well-lit areas.

Material and methods

40 coral colonies at risk of, or already affected by COTS predation in various state of degradation were selected for this study at Masaplod Sur Marine Protected Area, Dauin Municipality, Negros Oriental, Philippines. The reef has a distinct shallow area where coral density is higher, with many large *Acropora spp.* corals used for this study and a deeper end where corals become sparser and smaller (fig. 1).
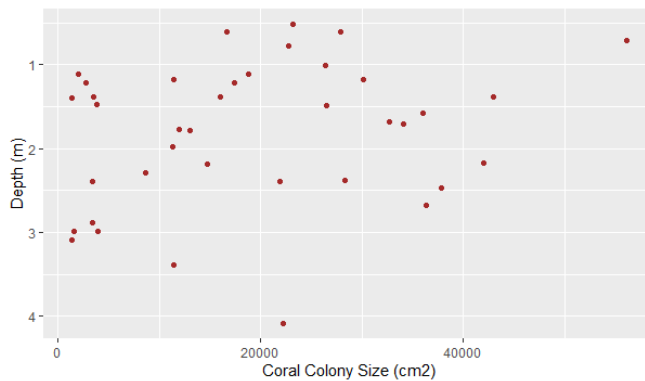

Fig. 1: Masaplod Sur MPA coral size distribution over depth. The reef has a distinct shallow bit with high diversity in genus and size, and a deeper portion where coral density becomes lower.

Of the 40 colonies selected, 38 were of genus *Acropora* and 2 were *Porites*. For the 38 *Acropora spp.* colonies, the whole colony and progression of feeding scars were photographed twice a week with an interval of 3-4 days using a GoPro Hero 6 Black with a 31 cm total length ruler located centrally on the coral for scale. For the two *Porites spp.* colonies, only COTS presence was noted due the complex 3D-structure of the colonies. Depth was recorded using dive computer readings at low tide at the approximate mid-level of the colony. All photographs were taken top down with the centre in the middle of the photo. In cases where colonies were too large to be fully captured in one photo, two or more pictures were taken in different areas top down to cover total area. Total colony size and feeding scars were identified and measured in ImageJ with the 31 cm ruler used for scale measurement. To account for deviations in photo angle and variations in image measurements, the total area for each coral is defined as the mean of areas measured from each picture. Areas affected by COTS predation were measured as the affected proportion of the whole coral and multiplied by the average colony size to get the predation-affected area. For some images there were perspective issues due to the nature of field work in shallow choppy waters and some areas of the coral were enlarged. To correct for this, identical affected areas were measured and averaged between all days present and newly affected areas were added to the corrected number for that day. In cases where COTS individuals are present on the corals on images and adjacent to new feeding scars, the area under the central disc would be considered affected as this likely ongoing predation. Feeding scars are primarily identified by large bright white areas with a distinct line where live coral tissue remains (fig. 2). This bright white (coral calcareous skeleton) is quickly colonised by filamentous algae after death and usually turns into a yellow colour after a few days followed by a darker brown after a few weeks.
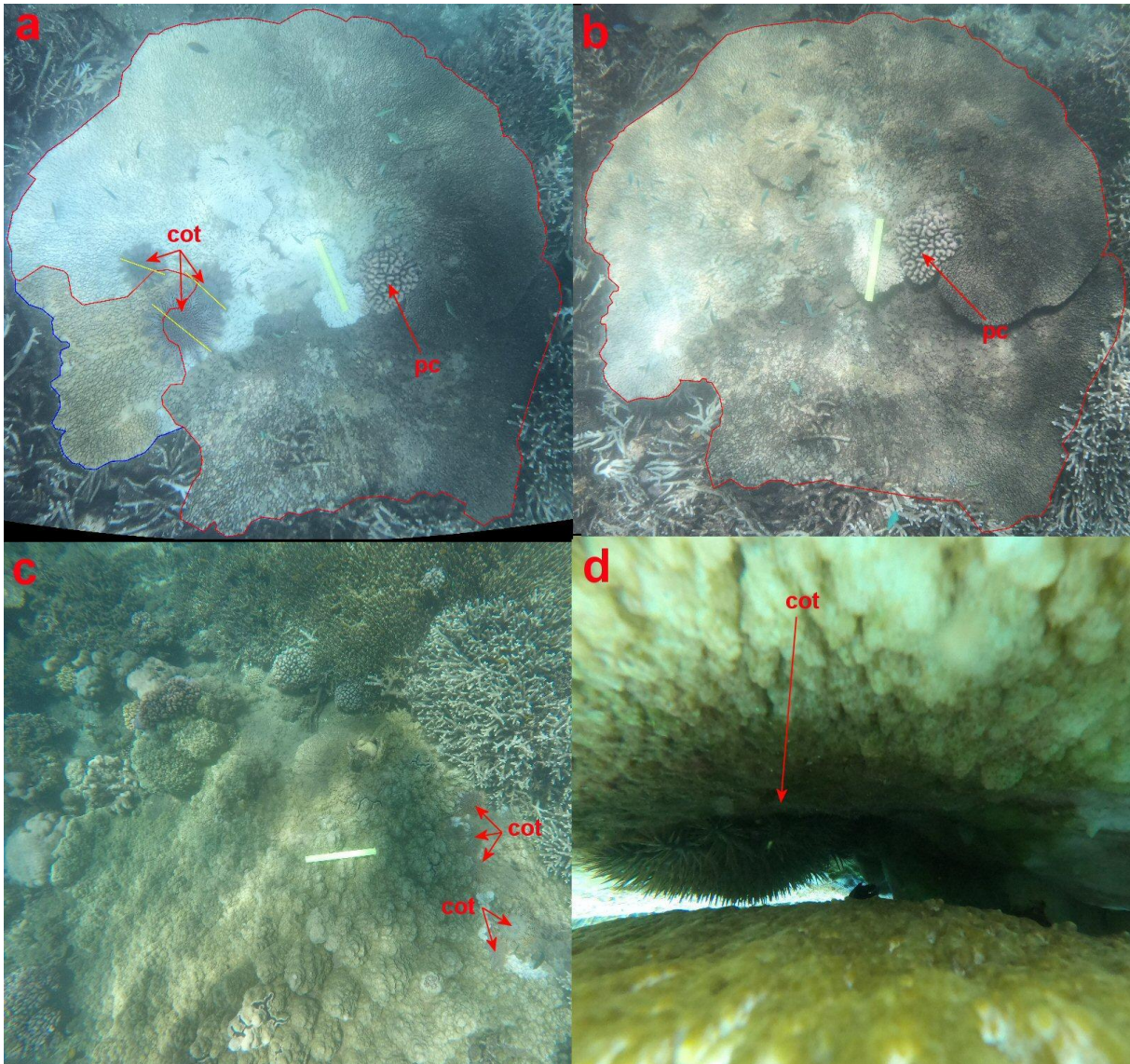
Fig. 2: Images used for size and feeding scar identification, images taken on (a) day 10 and (b) day 14. Day 10 (a) has three COTS (cot) present where the yellow lines measure the diameter relative to the yellow scale placed in the centre of the coral colony. Live coral is marked in blue and dead coral in red. Day 14 (b) is entirely dead as the remaining live tissue is freshly lost to COTS predation. This coral colony has an unaffected Pocillopora (pc) colony. Two massive Porites, one of which pictured in (c) were monitored for COTS presence but due to the complex 3D-structure could not be measured from photographs. (d) shows a COTS hiding under an affected Acropora colony.

The number of COTS present on each coral was noted as well as their location on the coral; above (whole COTS visible from above), edge (parts of the COTS visible from above), underneath (not visible from above) as well as COTS in close proximity but not in contact with colony (<0.5m away from any part of the coral colony). Numbered and coloured plastic flags were attached to dead coral close to the affected coral colony to identify individual coral colonies and mark their location.

The monitoring of the reef was divided into two periods: 17 days without any population control (cull) and after taking photographs on the 17th day, culling commenced and was repeated every 7 days. Initially for the pre-cull period images and COTS counts were taken in two different areas with the second area being monitored the day after the first, but as COTS densities decreased from culling, all colonies within the study area were monitored on the same day. Photographing continued regularly until the 34th day except for some corals where progression was tracked until complete tissue loss of the colony on the 45th day. Some data was recorded 7 days prior to formal starting day (Day 0; 10 May 2022) during method trials. Culls were done by a double injection of 20 ml (=40 ml total) vinegar,

using regular household vinegar (acetic acid content unknown) where both visible and hiding COTS were injected.

COTS individual predation rates were estimated based on the decrease in live coral area over the time period measured and the average COTS count from that day and previous measurement day. On days when culling was conducted, the same day's count would be put as 0 as all COTS on the coral in question were injected.

$$COTS\ predation\ rate = \frac{Difference\ in\ coral\ live\ tissue\ area}{Days\ progressed\ + \frac{COTS\ count\ +\ previous\ COTS\ count}{2}}$$

A model of the change in coral cover was created based on the mean of measured values and with linear regression on days when no measurement was done (fig. 3a; b). This is to estimate the rate of coral loss by keeping the regression slope constant between measurement days. The aim for this model is visualisation of the daily change as no measurements of COTS numbers or predation were taken on the days filled out by this visualisation model.

Statistical analysis was in R version 3.6.1 using built-in statistical analysis tools in RStudio version 1.2.5001 build 1468. All visualisations were done using the ggplot2 package version 3.3.2 and data was prepared using Microsoft Excel 365 version 2208.

Work done in collaboration with the Institute for Marine Research, Dauin Philippines including COTS culling equipment and planning – institutemarineresearch.org

Results

Coral cover change

During the total 45-day measurement period, coral loss due to COTS predation amounted to 24.57 m^2 on 38 *Acropora spp.* coral colonies, representing 33.9% of the total coral area. Most of the loss (17.41 m^2 or 24.0% of coral area) occurred in the first 17 days when no culls were done (fig. 3a; b). Coral loss on the 38 measured colonies averaged 333.8 cm^2 day^{-1} colony^{-1} before first cull and 76.76 cm^2 day^{-1} colony^{-1} during weekly culling (fig. 3c).

A contributing factor to the decrease in the coral loss rate is the increased rate of complete colony loss from ongoing COTS predation (fig. 3d), with the highest coral loss occurring in the first 10 days and complete colony loss in the first 14 days. The average live coral area on day 0 is 12,261 cm^2 or 55.8% of the colony but decreases to 5,795 cm^2 representing 24.5% of the total colony size. The highest estimated daily coral loss rate is 369 cm^2 colony^{-1} on day 8 (fig. 3c). Following the period of high coral loss, the number of dead colonies increases fast until the 15th day, after which culls begin and the number of dead corals increases at a much slower rate.
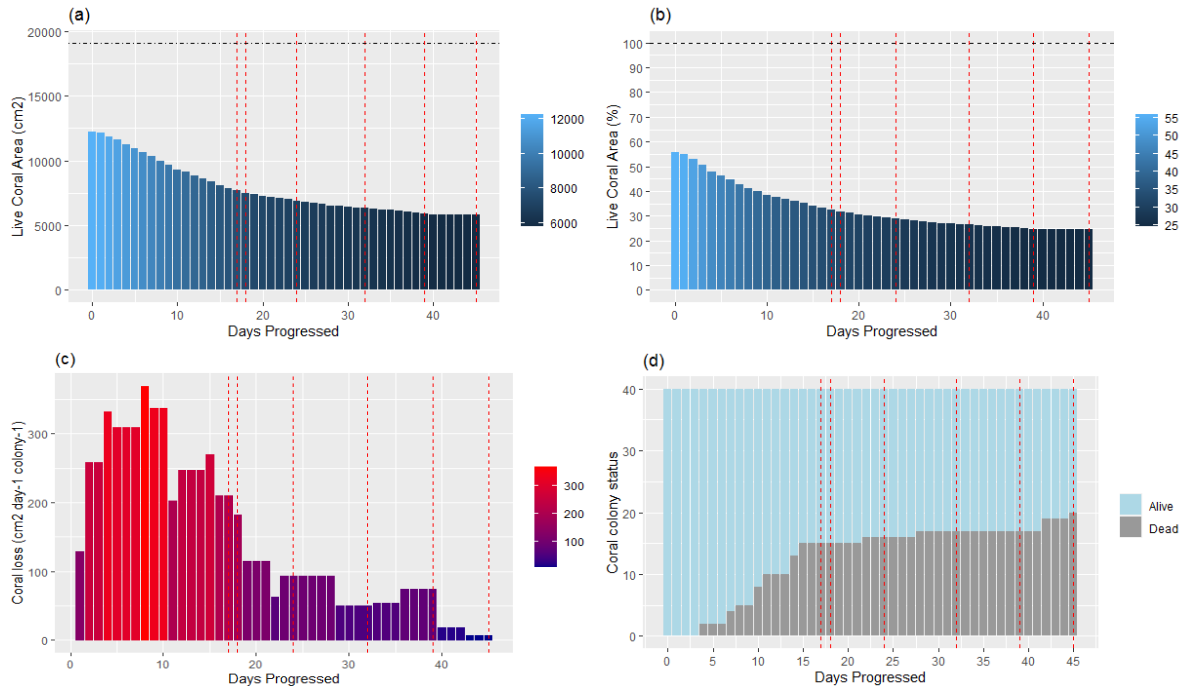
Fig. 3: Coral cover status for the monitored corals at Masaplod Sur MPA. Red dotted vertical lines show when culls took place, starting on day 17. (a) Average live coral area as measured on each of 38 corals with days between measurements plotted linearly, (b) proportion live coral, (c) measured and estimated average daily coral area loss for 38 corals (d) progression of coral colonies with any live coral area left (alive) or no live coral (dead) for 40 corals.

The first cull took place on day 17, followed by an additional cull on day 18 in another affected area of the reef, after which culls were done in all of the monitored area on day 24, 32, 39 and 45. Culling success was confirmed by routine sightings of collections of COTS spikes in very close proximity to where COTS had been injected during previous culls.

COTS population size and distribution

In total, 712 (650) COTS were recorded on the 40 (38 *Acropora spp.*) monitored corals between 7 days before day 0 and day 45. The highest number of COTS found on one day was 83 (76) on day 7 followed by 77 (63) on day 3. Numbers found decreased significantly in a weekly culling environment compared to pre-cull numbers (Wilcoxon rank sum test, $W = 28505$, $p < 0.0001$). Most COTS found on corals were underneath or hidden from view (fig. 4d), but there were less instances of COTS present anywhere on live corals after regular culling started, even between culls. When COTS are present however, a difference in the number of COTS per live coral in a weekly culling scenario cannot be seen (Wilcoxon rank sum test, $W = 1998.5$, $p = 0.6096$). Before any culling took place, a total of 108 (81) COTS were observed on top of the corals (average 0.53 per coral and day or 2.00 when any COTS presence). The proportion of COTS found hiding (fig. 4b) is higher when culls are ongoing (Pearson's χ^2-test, $\chi^2 = 79.785$, $df = 32$, $p < 0.0001$).
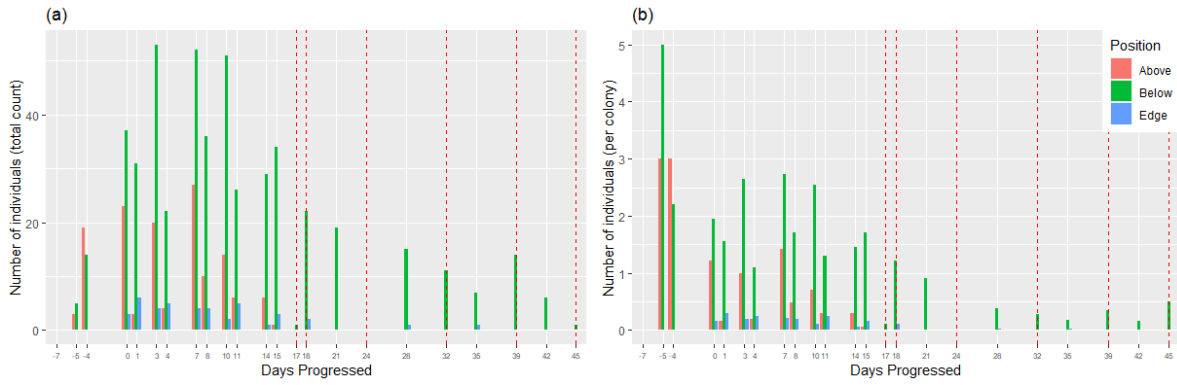
Fig. 4: Distribution of position COTS were observed on the coral (a) total per day and (b) average per coral colony monitored. Red dashed lines indicate when culls took place, starting on day 17. (Since monitoring started on all corals on day 0, the data on the days before display data for only a few colonies.) Most COTS are found underneath the tabulate Acropora colony but once culls are ongoing numbers found decrease significantly but COTS are also more likely to remain cryptic

The COTS counts on individual coral colonies range between 0-18 throughout the entire measurement period (fig. 5a) where higher COTS counts were found before culling commenced. The average COTS count at any time on the 40 (38) corals was 1.47 (1.43). When at least one COTS was found the average count was 4.05 (3.95; fig 5a). Of these, 74.3% would be found underneath the coral table or in crevices (cryptic).
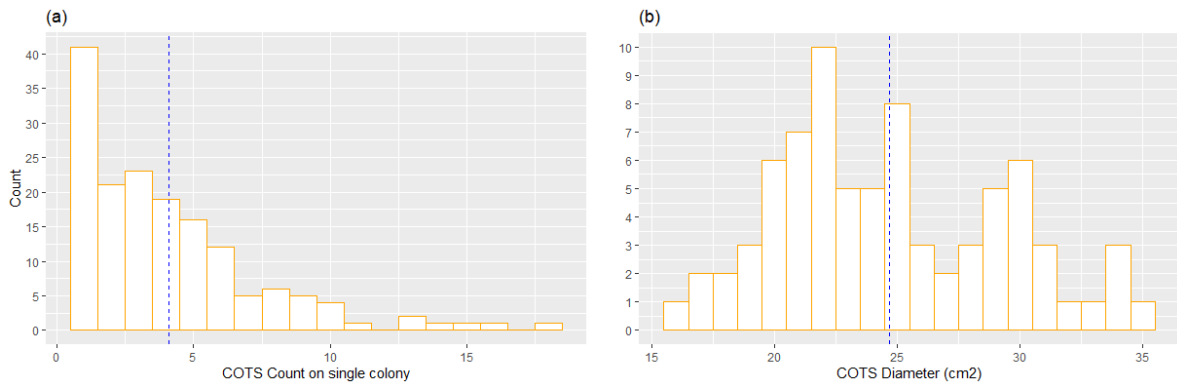

Fig. 5: (a) Frequency of COTS counts found on any of the 40 corals throughout the monitoring period, average count is 4.05, (b) diameter of COTS visible on top of corals ranging from 16.3 to 34.7 cm, average 24.7 cm marked with a vertical blue line.

Of the COTS visible on top of the coral colony, 77 individuals were found on a flat substrate enough to be measured. Diameters of these COTS ranged from 16.3 to 34.7 cm diameter (average 24.7 cm, fig. 5b). There were no clear correlations between the size of the COTS and where they were found, and they were not seen to be correlated to the total size of the coral or live or dead areas. No data was recorded on COTS underneath corals but they were observed to be of similar sizes.

COTS predation

Average estimated pre-culling individual predation rate was 126.1 cm^2 coral day^{-1} COTS^{-1} when coral loss was noted between days (period of active feeding). For the whole study period the estimated predation rate was 73.84 cm^2 coral day^{-1} COTS^{-1}, including days when no predation was detected. Post cull, the average estimated rate for periods of active feeding was 223.1 cm^2 coral day^{-1} COTS^{-1} when coral loss was detected, overall rate was 29.43 cm^2 coral day^{-1} COTS^{-1}. While culling of COTS contributes to considerable population decline and a decrease in coral loss (fig. 3), a difference in coral loss rate **for each instance of coral loss** cannot be seen (Welch Two Sample t-test, $t = 1.2428$, $df = 90.558$, $p = 0.2171$; fig 6a). However, the estimated individual COTS predation rate does appear to increase slightly in a culling environment (Welch Two Sample t-test, $t = -2.7307$, $df = 42.083$, $p <$

0.01; fig. 6b) but as there are less COTS on the measured corals post-cull, the overall predation rate decreases (Wilcoxon rank sum test, $W = 8368$, $p < 0.0001$).
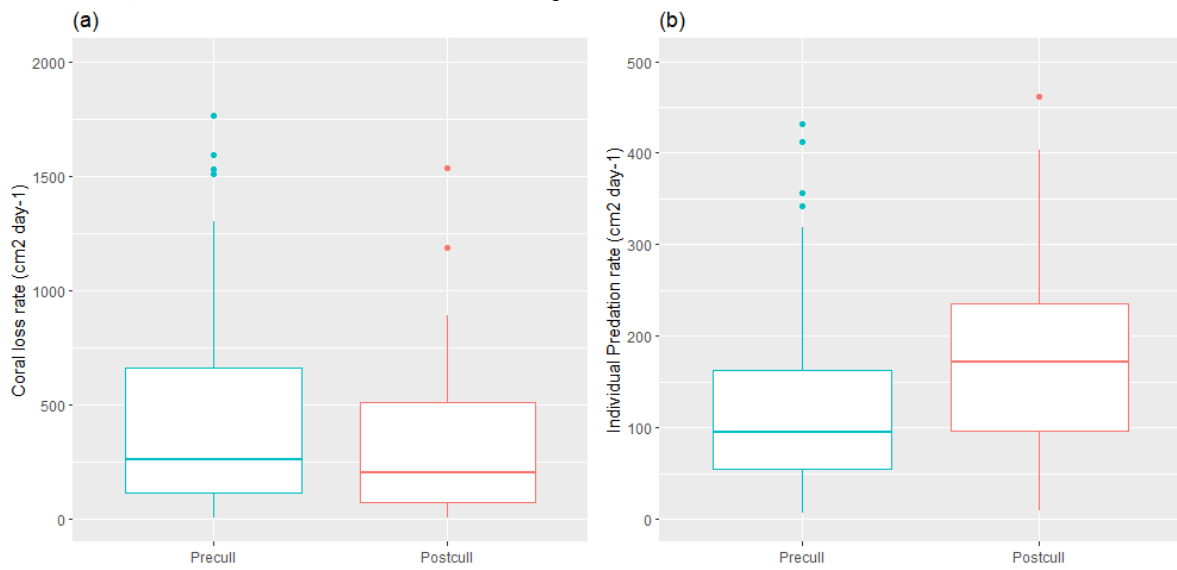

Fig. 6a: Average coral loss rate per instance of coral loss before and after first cull, b: estimated individual COTS predation rates before and after first cull.

From the images and data collected, there appears to be no density-related effect on average feeding rates of COTS present on corals (Pearson's moment-based correlation test = 1.0916, n = 153, df = 171, p-value = 0.2765; fig. 7). Pre-culling however a positive trend appears but the data spread is consistently high and most feeding rate estimates range between 0-300 cm^2 coral day^{-1} $COTS^{-1}$.
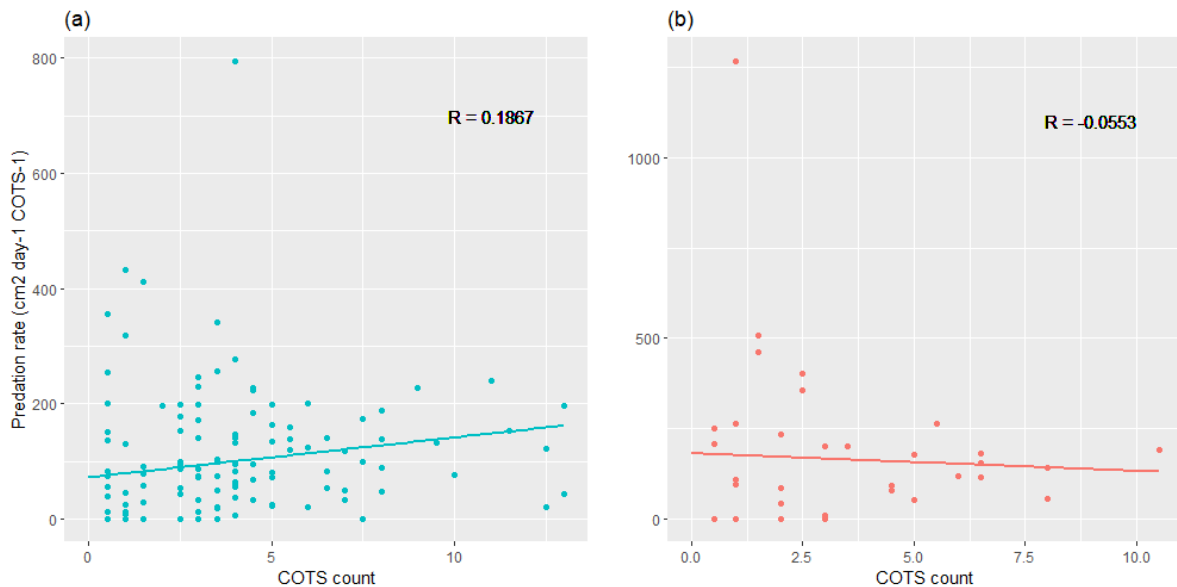

Fig. 7: Estimated individual feeding rates with corresponding average COTS count for the measurement period (a) pre-culling and (b) post-cull. Individual feeding rates appear to be mostly consistently varying between 0-500 cm^2 coral day^{-1} $COTS^{-1}$ with no clear correlation with COTS counts for the measurement period, even as COTS start to aggregate into tens of individuals on the same coral.

Discussion

Coral loss rates seen at Masaplod Sur MPA are very high over the short term and leave a long-term mark on a previously vibrant reef. The start of the outbreak is not exactly known but given the low proportion of live coral tissue on measured colonies, we estimate that COTS predation has been going on for a few months before the monitoring of the 40 colonies started. Coral loss rates are slightly less but similar to data recorded by Keesing and Lucas (1992), where summer consumption (similar temperature range) for similarly sized COTS (20-39 cm) recorded between 155-234 cm^2 coral day^{-1} $COTS^{-1}$ compared to average 126.1 pre-culling; 223.1 post cull in May-June at Masaplod Sur. Furthermore, previous studies report feeding rates as 378 cm^2 coral day^{-1} $COTS^{-1}$ (Chesher, 1969); 116-187 cm^2 coral day^{-1} $COTS^{-1}$ (Pearson & Endean, 1969), 148 cm^2 coral day^{-1} $COTS^{-1}$ (Glynn, 1973), 350 cm^2 coral day^{-1} $COTS^{-1}$ (Larkum, 1988), and highlights causes for variations such as COTS size, diet and season so these values serve as reference values only. This study has had a limited time-scope in the interest of starting culls fast to limit the reef degradation both from an ecological perspective but also that of local property owners and development activities, as the surrounding reefs are a big attraction for local tourism.

Of the COTS found on corals visible from above, diameter sizes range from 16 - 35 cm, average 24.7 similar to a previous report (24.2 cm, Chesher et al, 1969). While size cannot be accurately correlated with age but rather food availability and quality (Deaker et al, 2020a; 2020b) there is a noticeable lack of >35 cm COTS, estimated to be 3 years of age or older (after metamorphosis in lab conditions; Lucas, 1984). COTS have distinct growth phases where if fed coral, they grow fast and reach sexual maturity after 2 years when they measure around 20cm in diameter after which they grow slowly until they reach max size around year 3-4 at 30-45cm diameter (Lucas, 1984). Based on this and given the high food availability, the estimated age of the population at Masaplod Sur would be between 2-3 years since starting to feed on coral. Predation rates increase with diameter size (Keesing and Lucas, 1992) but no data could be collected on specific individuals' feeding rates in this study. What is worth highlighting here is that if no measures to reduce population size are taken COTS will continue to feed and grow, and individual predation rates will then increase as a result of individual growth.

The field methods used for this study are simple to deploy in remote locations and useful for tracking the progress of coral loss, especially useful in poorer-funded regions in the coral triangle. This study was done in the Philippines in collaboration with the Institute for Marine Research in Dauin, Negros Oriental province using existing surveying material. The ease of deploying this method is useful for conservation-oriented NGOs and environmental monitoring within and outside MPAs, but due to the simplicity of the model, there are significant drawbacks. Tidal state is important for getting images that capture the whole coral colony top down, but when surges are high and tidal state is low, getting images of the complete coral colony becomes difficult so the need arises to take several images to capture the entire coral colony. There is also the issue of angle as the camera and ruler used for scale are not fixed as to make the study minimally intrusive, which needs to be considered in the field. While several pictures are taken, typically in burst-shot mode, there will still be photos taken at a slight angle which will affect subsequent image analysis. There is therefore a constant need for data corrections, averaging and keeping known areas of the coral constant such as total size and consistently distinct areas like tiers or visible old feeding scars.

There were also complications measuring COTS feeding rates. Initial trials focused on marking individual COTS with tags, but COTS will shed tags regularly as Keesing and Lucas (1992) found in their study. Furthermore, COTS will naturally remain cryptic and use the complex coral environment to hide, making tracking of their movements difficult over several hours, let alone days. Instead, considering the generally slow movement speeds in high coral density environments (Keesing and Lucas, 1992), focus changed to fresh feeding scars on whole coral colonies where several COTS, typically remaining cryptic, would have recent coral loss attributed to them. The underside of tabulate corals would be the most accessible shaded area which COTS would be navigating to once they stop

feeding, meaning while food is still available COTS would be likely to be present, attracting more COTS due to chemical stimuli originating from ongoing predation (Hall et al, 2017).

Attraction to ongoing feeding could be the explanation why we observed the same coral colonies being predated on despite recent culls on the same colony and adjacent or proximal colonies not being affected either recently or at all. In essence, this could explain why colonies seem to be completely killed before predation begins on unaffected corals in high coral density areas. Despite knowing that COTS are attracted to ongoing feeding and will aggregate, there seems to be no clear correlation between COTS densities and individual feeding rates especially as densities increase into more than 7 COTS on a single coral colony (fig. 7). While there is intraspecific competition for food and COTS respond to this by aggregating, there is need for deeper investigation to explain why feeding rates as seen in this study do not seem to change with density. It is possible COTS are simply attracted to ongoing feeding and will move to where the stimuli comes from but only feed as needed. While size, which could not be measured on the majority of cryptic COTS, affects feeding rates, there are multiple factors contributing to why feeding rates could differ, such as movement, metabolic capacity, chemical stimuli and stress.

In this study, COTS were found to be hiding more when culls are ongoing, as no COTS were then spotted on top of the corals, only on the edge or underneath, in both cases not actively feeding (fig. 4). The reason for this is likely a result of chemical stimuli. As culls are happening, there will be less overall predation leading to less attraction to ongoing predation and aggregation of nearby COTS. While there was no clear change in feeding rates with density, larger and more productive corals are at greater risk of COTS predation when COTS will aggregate on a single coral until there is no live coral tissue left. While smaller conspecific corals would have a higher likelihood to remain unaffected, grow and reproduce, the sudden loss of larger, older corals would have negative effects on reef ecosystem and structure for very long periods of time. The aggregation of COTS on larger corals would also increase COTS spawning success leading to new outbreaks in the surrounding areas.

This study found individual feeding rates to increase post-cull when predation was detected, but decrease over the study period. A possible explanation to this is primarily the lack of aggregation caused by attraction to ongoing feeding. As COTS migrate to a single coral colony and remain in the vicinity due to stimuli attraction, less energy will be used for foraging which would result in lower metabolic demand and feeding rates. Conversely, with lower population densities and less ongoing predation, individual COTS need to move around more to find suitable feed, without the attraction from stimuli. This results in more energy exerted from foraging and an increase in metabolic demand, resulting in higher feed rates in lower population densities when feeding occurs. However, the constant attraction to stimuli means COTS will migrate rather frequently and incur a higher metabolic cost overall. Conversely, lower density COTS will have less attraction to ongoing predation and move less, resulting in less overall feeding.

Future research needs to confirm if there is any effect from dying or decomposing COTS which causes nearby COTS to become cryptic or move away from the stimuli. Such a response would be evolutionarily advantageous and would be similar to the response to predators by moving away from the stimuli (Hall et al, 2017). Significantly less COTS were found on any of the monitored corals when culls were ongoing but in this study it is impossible to say whether that is because of culls being very effective, COTS moving away from decomposing COTS or a combination of factors. Soft tissue from dead COTS was sometimes still present after 3-4 days after injections but had disappeared completely after 7 days, confirmed by sightings of dying COTS and collections of COTS spikes within the monitored area where culls were still ongoing. While culls cause a significant decrease in COTS population, it remains unclear whether this is deterring COTS aggregation.

Population control measures (culls) are typically laborious and despite our best efforts to inject any COTS visible, there was a constant influx of COTS from outside the monitored area, mostly likely from within the MPA. COTS predation never fully stopped on all of the monitored corals despite weekly culls and while overall predation rates did decrease this is likely partly a result of complete

coral colony loss and overall coral cover decreasing, leading to less COTS aggregation. In addition, while culling efforts continued past the end of the monitoring period, new feeding scars and further complete coral loss were reported on the monitored corals up to 50 days after. While our control efforts were unsuccessful in stopping coral loss in the MPA despite frequent culling within the monitored area, the significant decrease in coral loss achieved could be the best option to protect remaining coral in an area, as other actions like improvement of water quality is nearly unachievable (Westcott et al, 2020). Dauin municipality is heavily reliant on coastal areas for economic activity and while it has seen significant development over the last decade this would heavily contribute to worsening coastal water quality. As increased success of juvenile COTS is linked to increased nutrient input (Brodie, 2005; Uthicke et al, 2015), this leaves MPAs like Masaplod Sur vulnerable to increased frequencies of COTS outbreaks and removal of reproductive and aggregating individuals is key to avoid future COTS outbreaks (Beach et al, 1975).

In conclusion:
- While culls cause a drastic decrease in the overall COTS population, they only alleviate COTS degradation of reefs as COTS will hide and be out of reach for culling and outside COTS will aggregate to where feeding occurs. However, while individual feeding rates appear to increase slightly while culls are ongoing, this does not translate into bigger instances of coral loss over time and culls remain an effective method to decrease reef degradation.
- While the exact mechanism remains unknown, culls resulting in rapid decrease in COTS population density cause COTS to hide more. While this is likely a result of less attraction to ongoing feeding, there still could be other contributing factors like predator avoidance behaviours.

Acknowledgements

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