



Investigating The Effects of Reef Complexity and Coral Morphology on Crown of Thorn Abundance in Dauin, Philippines

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Abstract

Coral reefs are vital global ecosystems that are facing unprecedented decline. This is primarily due to anthropogenic disturbance and climate change. However, among these threats are crown-of-thorns starfish (COTS), of which contribute significantly to coral loss while capitalising on other pressures. Given the importance of reef complexity as indicator of reef health, this study aims to understand its role in influencing COTS abundance and investigates the relationship between reef complexity, coral morphology, and COTS abundance. This study revealed a significant relationship between COTS abundance and reef rugosity, indicating higher abundances in areas with lower complexity (LM: $T_{1,87} = -2.919$, P = <0.01; GLMer: $Z_{1,87} = -9.065$, P = <0.001). While no significant relationship was found between COTS abundance and coral morphology (LM: p = >0.05). Results suggested limitations in data collection may have contributed to this discrepancy. However, pioneering work has been conducted, and understanding these dynamics is crucial for effective reef management and implementing these new understandings with other technologies in order to reduce the impact of COTS.

Introduction

Often dubbed the rain forests of the sea, coral reefs are among one of the most important ecosystems in the world. This is in part because of its dense biodiversity, giving a home to over 25% of all marine life, but also because of the ecosystem services it provides (Knowlton et al., 2010, El-Naggar, 2020). Services such as food provision, carbon sequestration and extreme weather protection (Moberg and Folke, 1999). This therefore underlines the significance of coral reefs in creating a positive impact globally, and is especially true for tropical and subtropical nations (Hughes et al., 2003). In addition to this, they are of immense economic value with global estimates ranging from \$29.8 to \$375 billion per year, with coral reef fisheries alone estimated to contribute \$6 billion to this total (El-Naggar, 2020, Eddy et al., 2021). However, despite their ecological significance, coral reefs are facing an unprecedented crisis marked by their widespread, and rapid degradation and decline. The world has already lost half of its coral cover since 1950s and close to 60% could be lost by 2030 (Wilkinson, 2004, Eddy et al., 2021). With one study suggesting that there are no pristine reefs left (Pandolfi et al., 2003). Moreover, local initiatives tasked with protecting coral reefs over the last 30 years have failed to reverse regional scale declines (Hughes et al., 2003). Therefore, understanding the multitude of causes for coral reef loss is imperative, with two primary drivers standing out: anthropogenic disturbance and climate change (El-Naggar, 2020).

There are numerous causes for coral reef loss, however anthropogenic disturbance and climate change are the primary drivers posing immense damage (El-Naggar, 2020). Anthropogenic disturbance accounts for many threats to coral reefs such as pollution via sewage discharge and agricultural runoff, costal urbanisation, sedimentation, overfishing and damaging fishing practices such as dynamite fishing (RICHMOND, 2015, El-Naggar, 2020). Just one of these threats acting alone can cause unprecedented impacts to coral reefs. For example, overfishing can trigger significant direct and indirect effects on community structure, reducing both species populations and diversity, which can eventually lead to species extinction (ROBERTS, 1995). A study by Simpfendorfer et al., (2023) provides evidence of this indicating reef shark abundance has declined by 73% since human pressure began. With many reefs now becoming ray dominated, creating community imbalance and threatening ecological function. Likewise, climate change also harbours multiple threats to coral reefs, such as ocean warming and acidification, coral bleaching, and extreme weather events (Ateweberhan et al., 2013). Similarity to anthropogenic disturbance, just one threat caused by climate change can cause extensive damage. For example, ocean warming, which has caused multiple reoccurring mass bleaching events since 1980s, leading to high levels of coral mortality (Hughes et al., 2017). As just an rise of 0.1°C can increase regional bleaching events by 35% (Baker et al., 2008). Ultimately, within these two primary drivers lie many threats, many of which often interact with each other, worsening the situation. Furthermore, if left unaddressed, can cause ecosystem collapse, thereby ceasing their provision of ecosystem services and jeopardizing the livelihoods of millions of humans as well as marine animal communities (ROBERTS, 1995, Hughes et al., 2018, Simpfendorfer et al., 2023). Therefore, studying coral reef

health is essential for a comprehensive understanding of coral threats and effective management strategies to protect these vital ecosystems (Flower et al., 2017).

To better understand the stressors to coral reefs and how it affects them research often looks ways to determine and study indicators of coral reef health to implement effective conservation (Castro-Sanguino et al., 2021). One such indicator is structural complexity (Yanovski et al., 2017). Structural complexity is the overall threedimensional geography of an something and accounts for the physical topography of the area such as contour, for example, how rough a surface is (Graham and Nash, 2013b). It is often thought ecological habitats with greater structural complexity contain more species due to an increase in potential niches and shelter. This in turn promotes diversity and increased specie abundance (Yanovski et al., 2017, Torres-Pulliza et al., 2020). This is found to be especially apparent within coral reefs where reef-building corals aggregate to give a reef its morphology, thus creating a complex habitat. Furthermore, reef complexity shows indications it drives numerous functions directly linked to the resilience of these ecosystems (Dustan et al., 2013, Bozec et al., 2015). Overall, this indicates reef complexity is a useful measurement to understand reef health and identify areas of vulnerability and implement targeted conservation efforts (Yanovski et al., 2017).

Studying complexity could provide valuable insights into the ecological interactions and dynamics of certain coral threats such has the crown-of-thorns starfish (Acanthaster planci), hereafter referred to as COTS. COTS were first acknowledged as an important threat to coral reefs in the 1960s and have since become one of the leading causes of coral loss (among climate change and anthropogenic disturbance) (Deaker and Byrne, 2022). COTS are a corallivore species belonging to the class of Asteroidea (Ramah et al., 2021). What makes them so dangerous is their life history, as well as their ability to take advantage of climate change and anthropogenic disturbance and greatly exacerbate their impacts (Kamya et al., 2018). COTS are very destructive to coral due to their feeding behaviours and boom and bust population dynamics (Vine, 1973). For instance, COTS can rapidly consume coral tissue, with just one COTS able to consume up to 12 m² annually. Moreover, COTS are highly fecund, capable of producing millions of eggs per spawning event and under certain conditions outbreaks can occur. It has been documented their populations can increase from 1 COTS ha⁻¹ to more than 1000 COTS ha⁻¹ (Deaker and Byrne, 2022). And on top of this due to their toxic spines COTS have relatively few predators, potentially further increasing the odds for outbreaks to occur (Cowan et al., 2017).

The overarching threat COTS generate that severely impact reefs are their outbreaks, as COTS are a natural part of Indo-Pacific reef ecosystems (Potts, 1981). Although only declared a threat since the 1960s, outbreaks could be a natural part of their life stratagem (Vine, 1973). As *Acanthaster* ossicles were found within the great barrier reef (GBR) fossil record, suggesting potential outbreaks may have occurred up to 2000 years ago (Fabricius and Fabricius, 1992). There have been serval factors proposed to cause COTS outbreaks (Uthicke et al., 2015). One factor is overfishing, as studies suggest removal of predator pressure increases COTS densities. Finding densities to be 2.8-fold higher on reefs that have fisheries when compared to no-take marine reserves (Kroon et al., 2021). Whereas, another factor is warming waters, with studies suggesting a 2°C increase may shorten COTS larval development time by 30%. While additionally increasing the probability of survival by 240% (Uthicke et al., 2015). Although only two theories are mentioned here all theories are still debated upon and have been for 50 years (Kroon et al., 2021). For example, another study regarding overfishing suggests most COTS predators (e.g., *Arothron* pufferfishes) are not targeted and links between overfishing and outbreaks thus remain equivocal (Cowan et al., 2017). In addition to this, though control programmes have been implemented since the 1960s, most have had limited success (Kroon et al., 2021). However, what is for certain is that COTS are capitalising on these effects, with COTS responsible for ~42% of coral loss within the GBR alone. Moreover, outbreaks are becoming more frequent (Uthicke et al., 2015, Deaker and Byrne, 2022). Therefore, it is of high priority to advance our understanding of COTS behaviour and biology to improve management effectiveness and reduce or prevent future outbreaks (Pratchett et al., 2017).

Hence, this signifies the importance in understanding how COTS may distribute themselves in accordance with a reef's complexity and thus their abundance (Montalbetti et al., 2022). As reef complexity has shown to effect corallivore behaviour as previous studies have indicated that the loss of complexity is typically followed by a decline in butterflyfish (Coker et al., 2014). However, on the other hand declines in complexity have shown increased outbreaks of corallivorous Drupella in the GBR, as physical damage to the coral gives the snail a point of entry (Comming, 2009, China et al., 2021). Moreover, COTS have been shown to indicate selective feeding on certain coral morphologies such as tabular. Thus, highlighting another potential driver of COTS abundance as well as reef complexity (De'ath and Moran, 1998b). As coral morphologies, as well as how much there is of a particular morphology can influence differences seen in reef complexity between locations (Dustan et al., 2013). Therefore, the overall aim of this study was to investigate how reef complexity and coral morphology may influence COTS populations and their subsequent abundance and distribution. And hypothesised that a low reef complexity will increase COTS abundance and coral morphology particularly increased tabular levels will affect COTS abundance.

Methods

Study area

Data collection occurred in the Bohol Sea along the coastline of Dauin, a municipality situated within the Negros Oriental province, Philippines. Here 3 study sites were chosen in accordance with previously established SCUBA dive sites, that offered COTS presence as well as differing general surface complexities. Subsequent site creation was guided by a local research non-governmental organisation (NGO) in partnership with the local government called The Institute of Marine Research (IMR) Dauin, Philippines. This was due to their extensive local reef knowledge and long-term monitoring.



Fig. 1. Map showing the 3 study sites of this paper, located in Dauin, Philippines and within the Bohol Sea.

Data collection

All data collection was conducted via SCUBA diving on a 50 x 2 m transect using 3 different survey types: COTS survey, Benthic survey, and a Complexity survey. At each site a transect was placed at a random using randomly generated fin kicks. Then once a transect was placed it was reeled out parallel to the shoreline and all 3 types of survey were then conducted on said transect. This would then be repeated 3 times per site. Therefore totalling 3 transects and 3 COTS, Benthic and Complexity surveys per site. Lastly, the COTS and Benthic surveys were adapted from techniques used by the Australian Institute of Marine Science (Miller et al., 2009). And the Complexity survey and was adapted from IMR (Brand, 2020).

COTS Survey

COTS abundance was recorded via a number count using a slate as well as taking a photo using an Olympus Tough TG-6 camera. However, this was only done if the surveyor couldn't identify the species with certainty. Therefore, allowing for identification to occur within the dry lab. This survey employs a SCUBA search technique in a zig zag motion along the transect and moving forward at a steady pace as shown in Fig. 2. Furthermore, COTS count would be conducted once per transect.





Benthic Survey

To record morphology composition (percentage cover) a benthic survey was conducted. This was done by taking an image 50 cm above the transect at every 1 m interval using a GoPro Hero 5 with a 50 cm plum line attached with a fishing weight (Fig. 3.). This created 50 photos per transect with a consistent field of view throughout.



Fig. 3. Visualisation of benthic survey (top) as well as photo of survey being conducted within the field (bottom).

Complexity Survey

Coral reef structural complexity data was collected via a complexity survey using a stereo video system (SVS). The SVS was comprised of two labelled left and right GoPros Hero 8s at 0.9 m apart in a PVC dive housing attached to a 1 m aluminium rail with soldered handles (Fig. 5a.). For the survey the cameras were set to video recording at 1080p, 60 frames per second and then placed in their housing. The SVS was then held with the cameras facing towards to water's surface. Once at the transect the diver placed a 3D calibration ruler exactly 50 cm in length on top of the transect line in a horizontal position. Next, the diver then positioned themselves 2 m above the transect line using a dive computer attached to the SVS. Following this the diver would then put themselves at the start of the transect with the SVS now facing down and situated so one camera is directly above the transect line, and the other is 1 m to the left of the transect line. Next, the operator would fin at a steady pace along the transect to complete 1 pass. The diver would then turn around and repeat this process on the right side of the transect for a 2nd pass (Fig. 5b.). Finally, a 3rd pass would be executed in a sshape pattern making sure not to go outside the 2 m width of the transect, the rails' 1 m length would aid with judging this (Fig. 5c.).



Fig. 4. Point a. shows a photo of the SVS with a black dive computer and housed with 2 GoPros used in a complexity survey. b. Shows a visualisation of the 1st and 2nd pass in a complexity survey. c. Shows a visualisation of the 3rd pass in a complexity survey.

Data Processing

Benthic Processing

To process and analyse the raw benthic data a software called Coral Point Count with Excel extensions (CPCe) was used (Kohler and Gill, 2006). Using this software each photo would be individually uploaded and labelled by site, transect number and photo number. Once uploaded each photo would have 30 randomly generated points overlaid over it and under each point the substrate or coral morphology would be identified, see Fig. 4. 10 predetermined morphologies were selected for identification and were as follows: Rock, Sand, Rubble, Branching, Sub-Massive, Massive, Foliose, Tabular, Encrusting and Solitary. Next, once all 3 transects of a site had been completely identified the software was told to export the percentage cover of each morphology per site as well as Shannon-Weiner diversity into an excel sheet. This was repeated for each site creating creating 10 morphologies with percentage cover and 1 diversity value per site. This study used the Shannon-Wiener index as it is sensitive to species with low frequency, while Simpson's Index is not. As a result, species with low frequency tend to be represented poorly (Brown, 1988).



Fig. 5. Screenshot of CPCe software where 30 randomly generated points are overlaid for identification within a benthic survey photo.

Complexity Processing

The following complexity processing methodology was adapted from IMR (Brand, 2020). For complexity processing the videos from the GoPros were first edited to cut the videos into the 3 different passes made during the transect and labelled as such for both left and right cameras. These videos were then uploaded to software called VideoLAN Client (VLC) where the videos were transformed into photo stills at 2 frames per second (VideoLan, 2006). Following on from this the stills were further processed in RealityCapture 3D, a 3D modelling software using photogrammetric alignment to create a 3D model of the transect (CapturingReality, 2016). The photos were uploaded as folders of each pass and camera, an example folder would be named Poblacion_pass1_left_transect1. After photo alignment the calibration ruler would be found and control points placed on the calibration targets and its distance defined as 0.5 m. After this alignment was run again creating a 3D model (Fig. 6a.). Next, the 3D model was trimmed to that of the dimensions of the transect in real life (50 m \times 2 m), and a XYZ dense mesh point cloud was created, exported and uploaded to Gwyddion (Nečas and Klapetek, 2012). In Gwyddion the XYZ cloud was then rasterised, and empty space was removed by filling continuous empty areas with a mask before removing the mask that lay over the transect. Complexity was then calculated excluding the masked region by laying 5 simulated chains along the transect at 2, 1.6, 1.2, 0.8 and 0.4 m on the transect width. Gwyddion then measured each chain for surface distance and linear distance in order to calculate rugosity (a form of complexity measurement) using the following formula:

C = 1 - d/l

- C = complexity as rugosity
- d = surface distance
- l = linear distance

This consequently outputs a value between 0-1, with 0 being completely smooth and as the number increases so does surface roughness, with 1 being the roughest (Aronson and Precht, 1995). See Fig. 6b. for amplitude window showing Ra value (rugosity) from one chain. The mean of the each transect from each site was then calculated along with the standard deviation.





Fig. 4. a. Shows a 3D model of a transect in Poblacion 1 created using RealityCapture 3D. b. Shows Gywddion software measuring transect roughness as indicated by R_a.

Data analysis

All of the following statistical analysis and plot creation was performed on R version 2023.12.1+402 and RStudio (RStudio Team, 2020, R Core Team, 2024). Firstly, two scatter plots were created for data exploration and examination of trends within the distribution of COTS according to site, as well as how complex each site was. Next a bar plot was created to further explore the data and understand trends between morphologies. All subsequent plots were created using the ggplot2 R package (v3.5.0; Wickham, 2016). Another scatter plot was created using base R to compare "Rugosity" as a continuous explanatory to "COTS Abundance" as a discrete response. For statistical analysis visual inspection of a Q-Q plot using R package DHARMa and a distribution histogram highlighted a Poisson dispersal (v0.4.6; Hartig, 2022). Next a

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linear regression model (LM) was used for initial testing of significance and to explain changes in "COTS Abundance" (response variable) against "Rugosity", "Percentage Morphology" and "Diversity" (explanatory variables). In order to determine model of best fit, a backwards stepwise selection process was conducted and used each model's Akaike Information Criterion (AIC) score. The AICs were then compared against the null model (no explanatory variables) and the model with the lowest AIC score was chosen (Table 1). Following this, Model 1, highlighted in bold in Table 1 was chosen as the best model due to having the lowest AIC score. However, the LM didn't account for Site as a random effect therefore creating pseudo-replication. Thus, to account for this a Generalised Linear Mixed Effects Model (GLMer) with Poisson regression was used to test for significance and explain changes in "COTS Abundance" against "Rugosity", "Percentage Morphology" and "Diversity". To perform the GLMers the lme4 package was used (v1.1.35.1; Bates et al., 2015). Lastly, to determine model of best fit, a backwards stepwise selection process was used via each model's AIC) score. This then highlighted Model 12 as the model of best fit due to having the lowest AIC score (Table 2). Moreover, following the AIC tests, supplementary model testing via an overdispersion check using the R package performance, indicated model 12 also showed no overdispersion of residuals (v0.10.9; Lüdecke et al., 2021).

Model	Variables	AIC
Null	COTS Abundance ~ 1	486
1	COTS Abundance ~ Rock + Rubble + Sand	446
	+ Branching + Encrusting + Foliose +	
	Massive + Solitary + SubMassive + Tabular	
	+ Diversity + Rugosity	
2	COTS Abundance ~ Rubble + Sand +	449
	Branching + Encrusting + Foliose + Massive +	
	Solitary + SubMassive + Tabular + Diversity +	
	Rugosity	
3	COTS Abundance ~ Sand + Branching +	451
	Encrusting + Foliose + Massive + Solitary +	
	SubMassive + Tabular + Diversity + Rugosity	
4	COTS Abundance ~ Branching + Encrusting +	453
	Foliose + Massive + Solitary + SubMassive +	
	Tabular + Diversity + Rugosity	
5	COTS Abundance ~ Encrusting + Foliose +	454
	Massive + Solitary + SubMassive + Tabular +	
	Diversity + Rugosity	
6	COTS Abundance ~ Foliose + Massive +	458
	Solitary + SubMassive + Tabular + Diversity +	
	Rugosity	
7	COTS Abundance ~ Massive + Solitary +	458
	SubMassive + Tabular + Diversity + Rugosity	
8	COTS Abundance ~ Solitary + SubMassive +	461
	Tabular + Diversity + Rugosity	
9	COTS Abundance ~ SubMassive + Tabular +	462
	Diversity + Rugosity	
10	COTS Abundance ~ Tabular + Diversity +	466
	Rugosity	
11	COTS Abundance ~ Diversity + Rugosity	467
12	COTS Abundance ~ Rugosity	469

Table 1.	AIC table of L	M tested i	models with	model of	best fit (1	1) highlighte	ed in bold.
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Table 2. AIC table of GLMer tested models with model of best fit (12) highlighted in bold. Asterix represents modelsthat lower AIC scores but indicated negligible differences of 0.000012 within their scores.

Model	Variables	AIC
Null	COTS Abundance ~ 1	482
1	COTS Abundance ~ Rock + Rubble + Sand +	123
	Branching + Encrusting + Foliose + Massive +	
	Solitary + SubMassive + Tabular + Diversity +	
	Rugosity + Site as a random effect	
2	COTS Abundance ~ Rubble + Sand +	123
	Branching + Encrusting + Foliose + Massive +	
	Solitary + SubMassive + Tabular + Diversity +	
	Rugosity + Site as a random effect	
3	COTS Abundance ~ Sand + Branching +	123
	Encrusting + Foliose + Massive + Solitary +	
	SubMassive + Tabular + Diversity + Rugosity	
	+ Site as a random effect	
4	COTS Abundance ~ Branching + Encrusting +	123*
	Foliose + Massive + Solitary + SubMassive +	
	Tabular + Diversity + Rugosity + Site as a	
	random effect	
5	COTS Abundance ~ Encrusting + Foliose +	123
	Massive + Solitary + SubMassive + Tabular +	
	Diversity + Rugosity + Site as a random effect	
6	COTS Abundance ~ Foliose + Massive +	123
	Solitary + SubMassive + Tabular + Diversity +	
	Rugosity + Site as a random effect	
7	COTS Abundance ~ Massive + Solitary +	123
	SubMassive + Tabular + Diversity + Rugosity	
	+ Site as a random effect	
8	COTS Abundance ~ Solitary + SubMassive +	123
	Tabular + Diversity + Rugosity + Site as a	
	random effect	
9	COTS Abundance ~ SubMassive + Tabular +	123
	Diversity + Rugosity + Site as a random effect	
10	COTS Abundance ~ Tabular + Diversity +	123
	Rugosity + Site as a random effect	
11	COTS Abundance ~ Diversity + Rugosity +	123*
	Site as a random effect	
12	COTS Abundance ~ Rugosity + Site as a	121
	random effect	

Results

Overall, this study conducted 9 transects (3 per site), during which a total of 9 COTS surveys, 45 complexity measurements, 450 benthic photos and 13,500 Cpce analysis points were conducted to produce the following results.

Model 1	Variables	T value	p-value
	Rock	-1.806	0.0752
	Rubble	-0.351	0.7270
	Sand	-0.612	0.5423
	Branching	-1.612	0.1220
	Encrusting	-0.135	0.8930
	Foliose	0.384	0.7024
	Massive	0.406	0.6862
	Solitary	-0.083	0.9337
	SubMassive	-0.191	0.8492
	Tabular	-1.367	0.1760
	Diversity	1.506	0.136
	Rugosity	-2.919	0.00446

Table 3. LM results of Model 1

Table 3 represents the LM results from the best selected for model as determined via its AIC score. The results indicated that all morphologies showed no significant effect on COTS, and thus could not explain their abundance (p = >0.05). The same was true for diversity ($T_{1,87} = -1.506$, p = >0.05). However, model 1 did indicate rugosity did significantly affect their abundance suggesting increased abundances at lower rugosities ($T_{1,87} = -2.919$, P = <0.01). Although, Model 1 does not account for site as a random effect.

Table 4. GLMer results of Model 12

Model 12	Variables	Z value	p-value
	Rugosity	-9.065	<0.001

Table 4 shows the GLMer results from the model of best fit and indicates rugosity has a significant effect on COTS abundance ($Z_{1,87}$ = -9.065, P = <0.001). Thus, this allowed for a 99.99% confidence rate that variation in COTS abundance could be explained by rugosity (Fig. 7.). Table 4 does not include results of the other variables as for a GLMer the data set was too small causing collinearity due to a lack variation within the variables. Therefore, all morphology and diversity results from all the models gave an N/A output. Thus, the simpler model was chosen and due to its AIC score. However, as no results could be obtained from the GLMers for morphology and diversity the rest of this paper has used the LM results from Model 1 (Table 3) when presenting morphology and diversity. And the GLMer result for rugosity



Fig. 7. Scatter plot of COTS Abundance According to Rugosity. The blue line represents a regression line, and data points show mean rugosity measurements, each from 1 of the 9 transects. Vertical black lines are errors bars that show the standard deviation.

Fig. 7. Further solidifies rugosity had a significant effect on COTS abundance ($Z_{1,87}$ = -9.065, P = <0.001). Moreover, the blue linear regression line indicated a negative relationship between COTS abundance and rugosity, indicating as rugosity increases COTS abundance decreases. This can be seen further as COTS in abundance is only greater than 0 below 0.1 rugosity, particularly at 0.04 rugosity. The error bars in Fig. 7. represent the standard deviation and their small size implies each rugosity measurement is tightly clustered around the mean, indicating low variability in the data.



Fig. 8. Bar plot of Percentage Morphology According to Site. Each colour of the legend key represents 1 of 10 coral reef surface morphologies defined (observed better here?) within this study.

Fig. 8. Represents a bar plot showing the percentage levels of each morphology found within each site. Poblacion 1 shows the highest amount of diversity with a percentage level for all 10 morphologies. Whereas, both Masaplod Norte and Maayong Tubig show a similar but lower overall diversity, showing levels for only 7 morphologies. Although visual trends could be seen, diversity was shown not to significantly explain COTS abundance ($T_{1,87}$ = -1.506, p = >0.05). However, the two sites differ in morphology type found and their subsequent percentage levels, with Maayong Tubig indicating no levels of foliose but a level of 4% in tabular. And Masaplod Norte showing a level of 1.6% in foliose but no levels of tabular. Moreover, Masaplod Norte and Maayong Tubig both show high percentages of sand at 64% and 42% respectively, possibly indicating an overall smoother surface complexity. While Poblacion 1 shows a low percentage of sand (9%) and a very high percentage of branching (49%), as well as massive (11%), potentially indicating a rougher surface complexity. Although, Maayong Tubig also shows a high percentage of rock (30.5%). However, while trends could be seen via Fig. 8. All morphologies did not significantly explain COTS abundance (p = >0.05, see Table 3 for all results).

Discussion

This study found strong evidence in support of the hypothesis that COTS abundance is affected by rugosity, as an increased abundance of COTS were observed in areas of low complexity. This is in line with similar studies that found other corallivores such as drupella and the spiny cushion sea star to be more abundant in areas of lower complexity (Comming, 2009, Montalbetti et al., 2022). However, unexpectedly no strong evidence was found concerning COTS abundance and morphology, particularly with increased tabular levels. This is contradictory to similar studies that find coral form

heavily influences COTS feeding behaviours with a strong preference to tabular forms. As COTS are shown to prefer tabular 5x times as much as branching, submassive and foliaceous forms (De'ath and Moran, 1998b). Similarity, increased diversity also observed no significant evidence in effecting COTS. Although, on the other hand, these results conform to the literature as COTS show feeding preferences and thus would prefer to distribute themselves within areas with a lower diversity, and select for areas with higher preferred coral densities (Kenyon and Aeby, 2009, Li et al., 2023). Therefore ultimately, we can accept the hypothesis regarding rugosity and increased COTS abundance, but we must reject the morphology as well as diversity hypothesis and accept the null.

It has been hypothesised that larger corallivore starfish prefer low complexity reefs due to ease of movement, and studies suggest that larger specimens could be prevented from moving within complex reef frames (Montalbetti et al., 2022). For example, spiny cushion stars and their anatomical features have been hypothesised to represent a strong influencing factor in its distribution and habitat choice (Montalbetti et al., 2019). Thus, this could explain the differences seen in COTS distribution. However, the COTS in this study may have only been observed within areas of low complexity as they were larger individuals. Therefore were easier to spot during data collection, as COTS often conceal themselves within coral frames and crevasses (Rivera-Posada et al., 2014). Moreover, it has been well documented COTS and other corallivore invertebrates show increased movement during nocturnal conditions (Burn et al., 2020). Therefore, as data collection occurred during daylight hours, COTS abundances could have been missed. Although, the literature also shows evidence for increased movement ($\sim 20\%$) during the day for larger COTS when compared to smaller COTS (De'ath and Moran, 1998a). In general, echinoderms show a strict connection with reef structure due to different ethological aspects, and cryptic behaviour is often reported in corallivore echinoderms because of this (Dumont et al., 2007, Pratchett et al., 2017). Therefore, highlighting the importance of further research regarding COTS and their relationship to reef complexity. Particularly as the impact of complexity on invertebrates remains a relatively underexplored aspect (Graham and Nash, 2013a).

What was not expected from the results in this study were the non-significant results of the tabular morphology. However, this could be due to a lack of data therefore creating little variation and causing collinearity between morphologies. Thus, the variables may have not had enough statistical power to explain COTS abundance. Therefore falsely accepting the null (Bates et al., 1992). As similar study conducted by De'ath and Moran, (1998) performed statistical analysis using 2618 rows of coral morphology over an 18-month period. Whereas this study was conducted on 30 rows of coral morphology over a 4-week period. Moreover, rugosity was the only variable modelled within a GLMer. Therefore, accounting for site as a random variable and avoiding pseudo-replication. However, both diversity and morphology were modelled using a LM and may strongly suffer from pseudo-replication, further explaining the results seen. Therefore, interpreting these results must be taken with strong cautiousness (Hurlbert, 1984). Consequently, further work would benefit from an increased data collection period (Bates et al., 1992, Baguley, 2004). However, this study is pioneering work within COTS and highlights the importance of further study.

Studying COTS in relation to reef complexity could create scientific advances and potentially aid with predicating their distribution, as well as which reefs are more vulnerable and more likely to observe an outbreak (Pratchett et al., 2017, Montalbetti et al., 2022). Moreover, future complexity work could be combined with larval dispersal patterns using biophysical simulations to offer the best available insights into COTS patterns at large spatial and temporal scales. As evidence suggests larval dispersal and distribution is heavily influenced by hydrodynamics as well as substrate settlement (Doll et al., 2023, Bode et al., 2024). Therefore, understanding how and where COTS populations are founded is imperative in supporting management decisions (Bode et al., 2024).

In conclusion, this study provides strong evidence supporting the hypothesis that COTS abundance is influenced by rugosity, with increased abundance observed in areas of low complexity. This finding aligns with similar studies on other corallivores, suggesting a preference for habitats with a lower complexity. However, the lack of significant evidence regarding COTS abundance and morphology, contradicts previous studies suggesting a strong preference for tabular forms. While unexpected, this discrepancy could be attributed to limitations in data collection creating a low sample size and reducing statistical power. This emphasises the need for further research with larger datasets and extended study durations. Despite these challenges, this pioneering work sheds light on the intricate relationship between COTS and reef complexity, underscoring the importance of continued investigation in understanding COTS distribution and potential management strategies. Moving forward, integrating complexity studies with larval dispersal patterns using biophysical simulations could offer further valuable insights into COTS population dynamics within broader spatial and temporal scales, aiding in effective reef management and conservation efforts.

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