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Environmental Factors Influencing the Distribution of Crown of Thorns Starfish on the Great Barrier Reef

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Cover photographs: (front) Prime COTS habitat, without COTS, on Rib Reef. Image: David Westcott; (rear) Map of where samples were collected. Image: Dan Gladish.

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http://www.nesptropical.edu.au

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ACRONYMS

AIMS............. Australian Institute of Marine Science
ASI................ Average Severity Index
CCC .... Concordance Correlation Coefficient
COTS............ Crown-of-Thorns Starfish
CSIRO........... Commonwealth Scientific and Industrial Research Organisation
EotR.............. Eye of the Reef
FMP .... Field Monitoring Program
GLMM........... Generalised Linear Mixed Model
GBR.............. Great Barrier Reef
GBRMPA ...... Great Barrier Reef Marine Park Authority
LTMP .... Long Term Monitoring Program
MSE .... Mean Squared Error
NESP .... National Environmental Science Program
QPWS........... Queensland Parks and Wildlife Service
RHIS .... Reef Health Impact Surveys
TWQ............. Tropical Water Quality
%IncMSE...... Percent increase mean squared error

ABBREVIATIONS

C .... Celsius
c.................... circa
eq.................. equation
et al............... and others
e.g................. for example
exp................ exponential
ha.................. hectare
i.e.................. in other words
m.................. metres
mm................ millimetres
%.................. percent

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EXECUTIVE SUMMARY

This report uses statistical modelling to identify environmental factors that influence the distribution of Crown-of-Thorns Starfish (*Acanthaster cf solaris*, hereafter referred to as COTS) on the Great Barrier Reef (GBR). COTS are predators of hard corals and rank among the leading causes of coral mortality on the GBR today and are likely to remain so while ever reefs can sustain large stands of coral cover. Understanding which primary environmental factors influence the distribution of COTS, and in particular the response of COTS to bleaching (whether it be behavioural, movement, population response, or otherwise), could be fundamental to informing management decisions on COTS control and the protection of future coral. Specifically, this report investigates three main issues: (i) the environmental factors that influence COTS on reefs; (ii) the effect of bleaching on COTS currently and in the future; and (iii) preference of COTS in regard to bleached or unbleached hard coral sites on a reef.

In order to accomplish these goals, we used a generalized linear mixed model for reef and site scale analyses and a random forest model to complement inference at the reef scale. We investigated spatial environmental factors, temporal effects, bleaching variables, coral cover, and other additional variables that were available from environmental monitoring conducted as part of COTS control and GBR monitoring more generally. Our modelling strategy was to focus primarily on hard coral cover and bleaching factors, using additional variables to answer the question of which environmental factors influence observed COTS.

While the models are able to identify environmental factors that influence the observed abundance of COTS, the driving factor in our analysis in these models tended to be the location and timing of COTS outbreaks relative to the sampling, i.e. the abundance of COTS in outbreaking sites swamped the effect of other variables. In comparison to outbreak status, the models found relatively weak associations with benthos variables, habitat, and bleaching variables. This was primarily due to the variability in the data making it difficult to extract any signal besides spatial and temporal correlation.

We found that amongst the fixed effects in the models, hard coral cover was consistently a primary indicator of higher observed COTS counts. We found that bleaching was not as influential in the abundance of observed COTS, but we also noted that there is confounding of bleaching with hard coral cover.

Our results indicate that any management decisions to prevent coral loss should focus on the location of the outbreak, regardless of bleaching at a reef or site. Further, our results also indicate that particular environmental and habitat types are not informative regarding the locations of COTS *a priori*, save for hard coral cover.

1.0 INTRODUCTION

The Great Barrier Reef (GBR) is the largest coral reef system in the world, comprising thousands of individual reefs and encompassing an area of over 340,000 square kilometres. Listed as an iconic World Heritage Site, the GBR is important to multiple Australian industries (Furnas, 2003) and has enormous cultural significance to both its Traditional Owners and the broader Australian community. Coral reef systems are fragile, however, and the GBR is currently subject to a range of threats including climate change impacts, coral predation, pollution and storms (Bellwood et al., 2019, Hughes et al., 2019). The cumulative effect of these impacts is significant, with more than 50% of coral cover lost across the GBR between 1985 and 2012 (De'ath et al., 2012). Losses due to coral bleaching are accelerating due to climate change, with major events in 2016, 2017, and 2020, and few direct local management options (Bellwood et al., 2019). In contrast, predation of coral by Crown of Thorns Starfish (*Acanthaster cf solaris*, hereafter COTS) can be moderated through direct local management (Westcott et al., 2020).

Understanding how best to protect the GBR from cumulative threats requires an understanding of the spatial and temporal coincidence of impacts and an understanding of how they potentially interact. While cyclone damage can be severe, it is difficult to estimate the timing or spatial distribution of future risk. Coral bleaching, however, can be related to regional ocean temperature variations that are already being mapped (Liu et al., 2003). The spatial and temporal distribution of impacts due to outbreaks of COTS, similarly, follow patterns that have been monitored over years and decades (Vanhatalo et al., 2016). Estimating where the effects of bleaching and COTS damage overlap in time and space, and identifying whether the two processes interact to increase overall coral damage, is vital to an improved understanding of how these cumulative risks could be managed more effectively in future (Pratchett et al., 2014; 2017).

Coral bleaching can occur when water temperatures at a reef exceed the temperature tolerance of coral by 1 to 2°C over a period of at least 2-3 days (Berkelmans and Willis, 1999; Reaser et al., 2000). These events are becoming more common as average ocean temperatures rise (Claar et al., 2018), and are likely to worsen in frequency (Claar et al., 2018; Hughes et al., 2018a), severity (Hughes et al., 2018a; 2018b) and coral impact (Hughes et al., 2018b) in the future. In the clearest demonstration of this process to date, coral reefs around the globe experienced unusually severe back-to-back bleaching events in 2016 – 2017 (Hughes et al., 2018b; 2018c). During these events upwards of 70% of global coral reefs were exposed to some level of bleaching (Heron et al., 2017). Coral bleaching is of concern due both to direct mortality, and to potential effects on recovery of coral and motility of coral larvae (Hughes et al., 2017; 2019).

COTS are a large predatory echinoderm found throughout the Indo-Pacific Ocean region (Pratchett et al., 2014) where they occasionally exhibit large-scale population outbreaks; on the GBR four outbreaks of COTS have been observed since the 1960s. During such events, COTS densities on individual reefs experiencing outbreaks may increase from normal background density levels as low as c. 1 ha^{-1} to over 10 times that amount (Moran and De'ath, 1992; Vanhatalo et al., 2016; Westcott et al., 2020), and potentially over 7000 ha^{-1} (Dumas et al., 2020), with coral cover sometimes reduced by over 90% (Pratchett et al., 2014). This level of coral loss can have major ecosystem impacts, some of which may be permanent (Pratchett and Cumming, 2019). When combined with external pressures such as bleaching from climate change, coral cover recovery trajectories can be temporarily or permanently depressed (Haywood et al., 2019).

This depression of coral recovery may not only be cumulative, but the interaction between bleaching and COTS may also magnify their respective impacts. This might occur through the effect of warmer water on COTS population processes such as larval survival and growth, whereby predation patterns change relative to the availability of hard coral resources (e.g. Byrne, 2011; Caballes et al., 2017a, 2017b; Kamya et al., 2014; Uthicke et al., 2016). If COTS become more active or redistribute to better access remaining hard corals, then the impact of bleaching may be amplified.

Management to mitigate the impact of COTS, and of any additional bleaching impact stemming from a potential interaction with bleaching, would be enhanced if it were possible to *a priori* predict COTS distributions at reefs. To date, the spatial and temporal distribution of COTS across the GBR have been documented through the outbreak cycle (e.g. Hock et al, 2014; Vanhatalo et al. 2016; Australian Institute of Marine Sciences, 2019; Great Barrier Reef Marine Park Authority, 2020) while other studies have sought to understand the micro-habitat preferences of COTS on individual reefs or reef sites (e.g. Wilmes et al., 2019). However, there has been little focus on linking site-scale data to broader scale patterns. Recent studies have started to examine the effects of COTS on coral cover recovery after coral bleaching events (e.g. Haywood et al., 2019; Keesing et al., 2019), although the focus has been on coral cover rather than the response of COTS populations.

To successfully facilitate coral cover protection through targeted COTS control efforts across the GBR, we need to understand the habitat preferences of COTS and their responses to outside pressures such as bleaching. It is therefore critical to understand key environmental factors influencing the distribution and behaviour of COTS at site, reef and GBR scales. Here we seek to answer three specific questions:

1. What environmental factors influence the abundance of COTS across the GBR?
2. What is the effect of coral bleaching on current and future COTS abundance within those environmental factors?
3. Given the importance of hard coral cover, do COTS prefer bleached or unbleached coral sites?

We build on the modelling efforts of Vanhatalo et al. (2016) and answer these questions using a statistical modelling approach that controls for variability of COTS densities through space and time (e.g. variability between reefs and amongst years). Statistical modelling has been combined with a non-parametric modelling approach to determine the environmental factors that influence COTS as well as the effects of bleaching and hard coral cover.

2.0 METHODS

A statistical modelling approach was used to determine the influence of environmental factors on the distribution of COTS. In this section we describe our method for modelling COTS abundance as a function of environmental, spatial, and temporal covariates. We are especially interested in COTS abundance in relation to environmental features, including percentage hard coral cover and coral bleaching (both in terms of immediate severity and long-term effects). We examine these questions at both the reef and site scale. To appropriately describe this relationship, we develop a parametric generalized linear mixed model (GLMM) at both scales and a non-parametric statistical random forest model for the reef scale. The GLMM model is beneficial for understanding which environmental variables influence the distribution of COTS (either positively or negatively), while the random forest model is beneficial for identifying variables that are important for prediction. The methods complement each other in the sense that while the GLMM requires a distribution assumption, the random forest does not; whereas the random forest is weaker in identifying the relationship of covariates to COTS than the GLMM model. Because of the high variability and large proportion of zeros in COTS counts, data was aggregated to daily averages for the reef scale modelling, before applying a negative binomial GLMM and a random forest model. For site scale, we develop only the GLMM model.

2.1 Description of the Data

We incorporate data available from several monitoring programs, the Australian Institute of Marine Science (AIMS) Long Term Monitoring Program (LTMP), Great Barrier Reef Marine Park Authority's (GBRMPA) Eye on the Reef (EotR) surveys, and Queensland Parks and Wildlife Service (QPWS), GBRMPA's Marine Bioregions of the Great Barrier Reef, GBRMPA joint Field Management Program (FMP), and the COTS control program. We classify data into two protocols: Reef Health Impact Surveys (RHIS) data and manta tow survey data. RHIS is a standardized protocol for monitoring coral reef health, following the procedure established by Beeden et al. (2014) (Great Barrier Reef Marine Park Authority, 2014). Monitoring programs that provided RHIS data include GBRMPA EotR, QPWS, FMP, and the COTS Control Program. Manta tow surveys (Miller et al., 2003) are available from QPWS, GBRMPA EotR, and FMP. Additionally, bleaching index categories at a given reef were sourced via RHIS data and the LTMP data, standardized to 5 categories in accordance with Berkelmans and Oliver (1999) and Berkelmans et al. (2004) for the years 2016 and 2017. Shelf location for a reef was also obtained from GBRMPA.

RHIS data is available for the period 8 January 2012 through 6 February 2020. RHIS data is site, "point" based, surveys in which a 78.5m^2 circular plot is comprehensively surveyed. However, this means that while RHIS data is a relatively precise and accurate measure of conditions at the sample site, individual surveys may not be indicative of the reef as a whole. At the site scale, RHIS surveys generally are conducted 3 times. However, multiple RHIS samples may be taken at a reef for a given year. Our dataset incorporates on average 61 RHIS samples per reef scale observation, which is still only a small proportion of the overall reef. At each RHIS site, observed COTS are recorded along with environmental factors such as aspect, habitat, and benthos cover. RHIS data also incorporates bleaching average severity index, an aggregated measure combining severity and proportion of bleaching for the different coral types. Critically, RHIS observers are formally trained in using the protocol regardless of monitoring program (Westcott et al., 2020).

Manta tow surveys are conducted by towing a diver behind a small boat at a set speed, with the diver recording data via visual inspection. Manta towing surveys cover a large area of the reef quickly and, while considered accurate (e.g. De'ath, 1991), likely exhibit lower precision and accuracy than RHIS surveys. Observed COTS and hard coral cover percentage were obtained from manta tows. Manta tow data was available from 29 November 2012 through 3 February 2020. Importantly, manta tow data and RHIS data were collected separately, although there was usually strong spatial and temporal overlap (i.e. different sites at the same reef in the same year).

2.1.1 Reef Scale Model Data

Table 1 lists the covariates we use for the site-specific and reef-specific models. For the reef scale models, preference is given to variables from the manta tow data as that dataset incorporated more information pertaining to the whole-of-reef. For that reason, the response variable for reef scale models was observed COTS counts from manta tows. COTS from manta tow data were aggregated by taking the total number of COTS counted for all the manta tows from a specific vessel on one day at a given reef. Because of this summation, we include a variable, *N*, the number of manta tows. This *N* serves as an offset and acts as a correction term in the model to account for the varying number of manta tows contributing to each observation.

Additionally, manta tow data incorporates hard coral percentage and for this we use two measures: mean hard coral cover and average Euclidean distance of hard coral cover of the aggregated manta tows (Eq. 1) at a reef. This latter measure allows us to account for the variation in the observations around the observed mean at a reef. For example, an aggregation of 0%, 50%, and 100% and an aggregation of 45%, 50%, and 55% hard coral cover from manta tows will have the same mean hard coral cover value, but the former will have a higher "distance" value accounting for the variation in hard coral cover percentage. The distance measure is calculated by:

$$\frac{2}{N(N-1)}\sum_{i\neq j}\left(c_i - c_j\right)^2 \qquad (1)$$

where c_i is the hard coral percent for manta tow i and N is the number of aggregated manta tows.

Benthos cover variables and bleaching averaged severity index for the reef scale models are obtained from the RHIS dataset. To ensure adequate representation at the reef scale, noting that individual RHIS observations are site-specific, we aggregate macroalgae, rubble, and bleached average severity index to the reef/year level. We do this by determining which RHIS observations were recorded at the same reef during the same year and taking the mean of the relevant covariates.

Table 1: List of covariate variables used for modelling including data source.

Variable	Description	Data Source	Model used
N	Number of manta tows used in observation aggregate	Manta tow	Reef
bleached_ASI	Bleached Average Severity Index from RHIS data	RHIS	Reef/Site
bleach_cat	Bleaching category of a reef in 2016 or 2017	RHIS/LTMP	Reef/Site
mean_cover	Mean hard coral cover of aggregated manta tows	Manta tow	Reef
dist_cover	Mean Euclidean distance of hard coral cover within aggregated manta tows	Manta tow	Reef
hard_coral_cover	Total hard coral cover percentage	RHIS	Site
rubble	Proportion of total benthos cover that is rubble	RHIS	Reef/Site
macroalgae	Proportion of total benthos cover that is macroalgae	RHIS	Reef/Site
habitat	Habitat of observation (e.g. reef flat, slope, lagoon, crest)	RHIS	Site
aspect	Majority cardinal direction (N, NE, E, SE, S, SW, W, NW)	RHIS	Site
shelf	Reef shelf location (inner, mid, or outer)	GBRMPA	Reef/Site
latitude	Spatial variable indicating latitude	RHIS/Manta tow	Reef/Site
latband	Latitude band	RHIS/Manta tow	Reef/Site, random forest only
reef_id	Reef Id categorical variable	RHIS/Manta tow	Reef/Site, GLMM only
year	Year of observation for associated manta tow and RHIS	RHIS/Manta tow	Reef/Site

Spatial variables include shelf, Reef ID and latitude. Shelf is a categorical variable indicating a reef's position on the GBR shelf; either inner-, mid-, or outer-shelf. Reef ID is a categorical variable indicating the specific reef of interest, represented by a two-digit number referencing the latitude band followed by a three-digit number representing the featured reef. Latitude is obtained by taking the average of the aggregated manta tows for a particular datapoint. Latitude band is the associated first two digits of the reef ID. We use latitude band as a substitute for reef ID in the random forest modelling primarily due to limitations of the random forest implementation, noting that the random forest model is meant as an enhancement to the GLMM model (see below).

Bleaching is captured through two variables: (i) Bleaching average severity index and (ii) a lagged effect of bleaching which we refer to as bleaching category. The bleaching average severity index is an aggregated measure of severity of bleaching and proportion of bleaching. It is calculated by codifying the bleached severity (where higher numbers indicate more significant bleaching) for a coral lifeform, and then multiplying it by the proportion of bleached coral. These are then summed together to create the bleaching average severity index. Bleaching category takes into account the temporal effects of bleaching, specifically on the widespread bleaching events of 2016 and 2017. Data from 2017 were assigned a bleaching category for the reef from 2016, if available. Data from 2018 onward were assigned bleaching category from 2017, if available. If 2017 was not available, then said data was assigned the bleaching category from 2016. This differs from bleaching average severity index in that this categorical variable is intended to provide some indication of the long-term effects of bleaching on COTS, whereas the average severity index is given at the same time as the COTS count. Because of this distinction, we only consider either bleaching average severity index or bleaching category for one model, not both (see below). Further, since bleaching category is based on the bleaching events from 2016 and 2017, models that include this variable only consider data from 2017 onward (not 2016).

2.1.2 Site Scale Model Data

Site-scale model data focuses at the sub-reef scale data, including observed COTS counts and hard coral cover percentage, coming from the RHIS dataset. Benthos cover variables rubble and macroalgae and bleaching averaged severity index do not need to be aggregated as in the case with the reef-scale data. Further, since the focus for this analysis is at this site scale, we also incorporate additional variables such as aspect and habitat. Aspect is a categorical variable that indicates the cardinal direction of the site with respect to its location on the reef. Habitat is also a categorical variable indicating the general habitat, i.e. lagoon, reef flat, or crest, that the RHIS site is on.

Spatial variables such as Reef ID, latitude, and latitude band are treated similarly to the reef scale data models, except that latitude is not averaged and references the latitude of the RHIS site observation. Bleaching category is also the same as that of the reef scale data models and references the reef bleaching category.

2.2 Zero-Inflated Negative Binomial Regression Modelling

We utilize a GLMM framework (Stroup, 2012) as a means of determining potential variables that are correlated with a significant increase or decrease in observed COTS for the reef-scale and site-scale data. Given the high number of zeros in both the reef-scale and site-scale data, and the discrete nature of the COTS count data (Figure 1), a reasonable distributional assumption is one of a negative-binomial distribution mixed with a point mass at zero. Therefore, we fit a zero-inflated negative binomial GLMM (e.g. Bolker, 2015). For COTS counts y, the model is:

$$y \sim \begin{cases} \theta + (1-\theta)NegBin(r,p), & y = 0 \\ (1-\theta)NegBin(r,p), & y > 0 \end{cases}, \tag{2}$$

where r and p are parameters associated with specifying the negative binomial distribution (commonly referred to as the number of successes and probability of success), and θ is the zero-inflation probability. In this framework, the mean μ and variance σ^2 of the negative binomial portion of the model are

$$\mu = \frac{rp}{1-p},$$
$$\sigma^2 = \mu\left(1 + \frac{\mu}{r}\right). \tag{3}$$

Following the GLMM framework, we then model the zero-inflation parameter, mean, and variance through:

$$g_1(\mu) = \boldsymbol{X_1\beta_1} + \boldsymbol{Z_1b_1} \tag{4}$$

$$g_2(\sigma^2) = \boldsymbol{X_2\beta_2} + \boldsymbol{Z_2b_2} \tag{5}$$

$$g_3(\theta) = \boldsymbol{X_3\beta_3} + \boldsymbol{Z_3b_3} \tag{6}$$

where $\boldsymbol{X_i}$ and $\boldsymbol{Z_i}$ ($i = 1,2,3$) are the matrices containing the fixed and random effects, respectively, with $\boldsymbol{\beta_i}$ and $\boldsymbol{b_i}$ being the respective vectors of covariate coefficients for the fixed and random effects. For a negative binomial distribution, $g_1(\cdot)$ and $g_2(\cdot)$ are log functions while $g_3(\cdot)$ is the logit function.

For our modelling purposes, we model $g_1(\cdot)$ as some combination of the parameters described in Table 1, leaving $g_2(\cdot)$ and $g_3(\cdot)$ to be modelled using only an intercept. These models are fit using the "glmmTMB" package (Brooks et al., 2017) in the R statistical programming language (R Core Team, 2020).

2.3 Random Forest Modelling

In addition to fitting a GLMM, we consider also a random forest-based model (Breiman, 2001) for the reef-scale data. Such a formulation may be considered non-parametric, and as such does not require a distributional assumption like that of the GLMM-based method. A random forest is a collection of classification and regression trees that creates a weighted average in order to predict a response variable after training. That is, for a collection of decision trees, f_b, a prediction of the response, y, can be obtained via

$$\hat{y} = \frac{1}{B}\sum_{b=1}^{B} f_b(\boldsymbol{x}), \tag{7}$$

where B is a predetermined number of trees. Critically, each tree is built via a random subset of covariates. From this method, we can obtain an importance measure for each covariate in prediction of the response. For full details, we refer the reader to Breiman (2001). Our implementation uses the “randomForest” package (Liaw and Wiener, 2002) in the R statistical programming language (R Core Team, 2020).

2.4 Model Formulation

Our strategy for model formulation is to focus primarily on the effects of bleaching and hard coral percentage, while incorporating additional fixed effects and accounting for spatial and temporal correlation where appropriate. To this end, we use 2 primary models for the reef-scale and site-scale data and create a series of subsets from those models.

Our model follows a mixed effects formulation for the GLMM with a simple additive structure for the random forest (noting that the GLMM is inferential, whereas the random forest model is predictive). The random effects portion of the GLMM accounts for spatial and temporal correlation. For ease of comparison, we formulate the spatial and temporal effects similarly for the random forest model, though the random forest model does not estimate the variance components as in the GLMM. We formulate the spatial and temporal effects differently in the GLMM and the random forest model. These are:

$$\mathrm{RE}_{glmm,ij} = \mathrm{year}_j + \mathrm{reef\_id}_i + \mathrm{reef\_id}_i \times \mathrm{year}_j,$$

$$\mathrm{RE}_{rf,ij} = \mathrm{year}_j + \mathrm{latitude\_band}_i \times \mathrm{year}_j,$$

where RE_{glmm} and RE_{rf} refer to the spatial and temporal effects for the GLMM and random forest models, respectively. Importantly, the reason for including reef_id as a random effect in the GLMM is that it allows for diversity of underlying fundamental characteristics of individual reefs (e.g. morphology, exposure to meteorological and oceanographic conditions), incorporating the variability amongst and between reefs within our modelling framework. Incorporating a year random effect allows for varying climatic responses across time. The interaction random effect allows for a spatio-temporal variability, accounting for the fact that different reefs potentially will respond differently through time (for example, to climate drivers). The reason for using latitude band as opposed to reef_id for the random forest model is primarily due to limitations of the randomForest package in R, specifically the number of categories for reef_id is higher than what the randomForest package allows. Using this formulation, however, still allows for spatio-temporal variability to be incorporated into the random forest model, albeit at a coarser resolution. To account for the differences described above with bleaching, we create two general formulations: M1 and M2. M in this context refers to R or S, representing reef-scale models or site-scale models. M1 models use bleached average severity index while M2 models use the lagged bleaching category variable.

The models for the reef scale data are as follows:

$$\begin{aligned}\mathrm{R1.0}: f(y_{ijk}) = \beta_0 &+ \log(\mathrm{N}_{ijk}) + \mathrm{bleached\_ASI}_{ijk} + \mathrm{mean\_cover}_{ijk} + \mathrm{dist\_cover}_{ijk} \\ &+ \mathrm{rubble}_{ijk} + \mathrm{macroalgae}_{ijk} + \mathrm{shelf}_i + \mathrm{latitude}_i + \mathrm{RE}_{ij} + e_{ijk},\end{aligned}$$

$$\begin{aligned}\mathrm{R1.1}: f(y_{ijk}) = \beta_0 &+ \log(\mathrm{N}_{ijk}) + \mathrm{bleached\_ASI}_{ijk} + \mathrm{mean\_cover}_{ijk} + \mathrm{dist\_cover}_{ijk} \\ &+ \mathrm{rubble}_{ijk} + \mathrm{macroalgae}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},\end{aligned}$$

$$\text{R1.2: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleached\_ASI}_{ijk} + \text{mean\_cover}_{ijk} + \text{dist\_cover}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{R1.3: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleached\_ASI}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{R2.0: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleach\_cat}_{ijk} + \text{mean\_cover}_{ijk} + \text{dist\_cover}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \text{latitude}_i + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{R2.1: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleach\_cat}_{ijk} + \text{mean\_cover}_{ijk} + \text{dist\_cover}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{R2.2: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleach\_cat}_{ijk} + \text{mean\_cover}_{ijk} + \text{dist\_cover}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{R2.3: } f(y_{ijk}) = \beta_0 + \log(\mathrm{N}_{ijk}) + \text{bleach\_cat}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

where i is the index for reef, j the index for year, and k the index for aggregated manta tow observation. We use y_{ijk} as the given total COTS observed for the GLMM and log of COTS for the random forest at reef i, year j, and manta tow k, and RE_{ij} to reference the formulation of "random effects" as described above. Further, e_{ijk} is the associated measurement error term. We include the term N_{ijk} on a log scale to account for the number of manta tows in each observation. Thus, we can think of these models as the number of COTS per log of the number of manta tows. We note that $f(\cdot)$ is a generic function term referencing either the GLMM or random forest model.

The site scale models follow similar logic and are as follow:

$$\text{S1.0: } f(y_{ijk}) = \beta_0 + \text{bleached\_ASI}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \text{aspect}_{ijk} + \text{habitat}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \text{shelf}_i + \text{latitude}_i + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S1.1: } f(y_{ijk}) = \beta_0 + \text{bleached\_ASI}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \text{aspect}_{ijk} + \text{habitat}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S1.2: } f(y_{ijk}) = \beta_0 + \text{bleached\_ASI}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S1.3: } f(y_{ijk}) = \beta_0 + \text{bleached\_ASI}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S2.0: } f(y_{ijk}) = \beta_0 + \text{bleach\_cat}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \text{aspect}_{ijk} + \text{habitat}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \text{latitude}_i + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S2.1: } f(y_{ijk}) = \beta_0 + \text{bleach\_cat}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \text{aspect}_{ijk} + \text{habitat}_{ijk} + \text{rubble}_{ijk} + \text{macroalgae}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S2.2: } f(y_{ijk}) = \beta_0 + \text{bleach\_cat}_{ijk} + \text{hard\_coral\_cover}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

$$\text{S2.3: } f(y_{ijk}) = \beta_0 + \text{bleach\_cat}_{ijk} + \mathrm{RE}_{ij} + e_{ijk},$$

where i is the index for reef, j the index for year, and k the index for RHIS site.

Regarding the sub-specifications Mx.0, Mx.1, Mx.2, and Mx.3 (where x represents 1 or 2), Mx.0 includes all interested variables, whereas the remaining models are subsets of Mx.0. Mx.1

removes some spatial characteristics such as shelf, aspect, and latitude variables, where appropriate. Mx.2 further removes all other environmental variables, leaving only the hard coral cover and bleaching variables. Mx.3 then removes the hard coral cover variables to look only at bleaching effects.

3.0 RESULTS

The reef-scale data aggregated to 1443 different observations, while the site-scale data was available for 18704 different RHIS sites. Histograms of the observed COTS counts for both the reef-scale and site-scale are found in Figure 1. We apply the models described in Section 2.4 using the GLMM and random forest models described in Sections 2.2 and 2.3 for the reef-scale data, and the GLMM for the site-scale data.

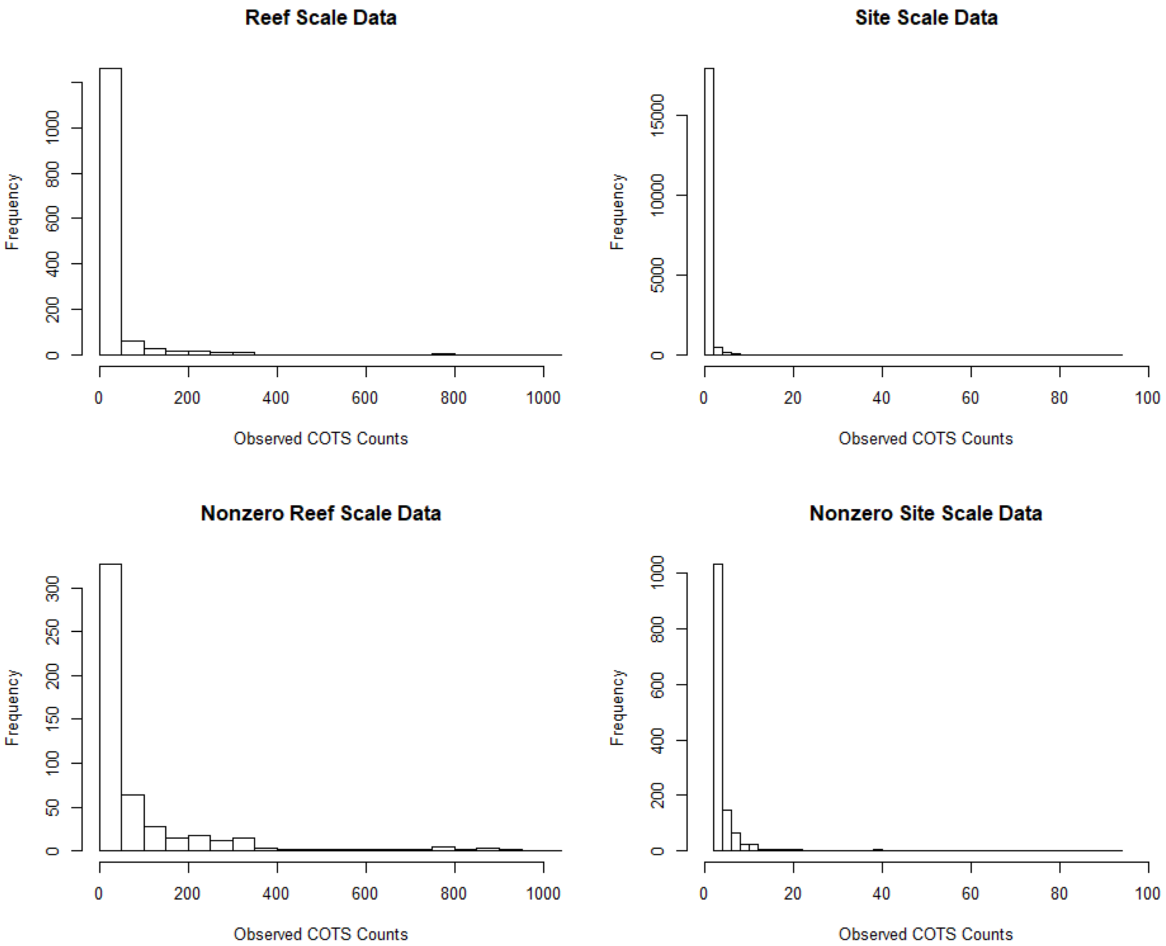


Figure 1: Histogram of observed COTS counts for the reef scale (left) and site scale (right) data. Top row shows the full data while bottom shows data with at least one COTS observed. Reef scale incorporates data from 11 Nov 2012 through 3 Feb 2020 between latitudes -12.832 to -24.114. Site scale incorporates data from 8 Jan 2012 through 6 Feb 2020 between latitudes -12.919 and -24.120.

3.1 Model Performance

We first fit the zero-inflated negative binomial mixed model and random forest to the observed COTS in the reef-scale data, and then assess model performance on the data. We consider model performance from two perspectives: model fit and variance explained.

To examine the model fit performance, we compare the observed COTS abundance to the predicted abundance. We then look at the R-squared values of a simple linear regression of the fitted COTS to the observed COTS. We also look at Lin's concordance correlation coefficient (CCC) (Lin 1989). CCC is a measure of agreement between two datasets between

0 and 1. Higher values indicate better agreement. We also look at the variance of COTS explained by the random forest model. These values are found in Table 2 along with the mean squared error (MSE). In general, the zero-inflated negative binomial model performs better when looking at the R-squared values, but worse when comparing the CCC and MSE values. This is primarily due to the zero-inflated nature of the data. The GLMM is performing better at determining zero values while the random forest model performs better with the non-zero portion of the data. This is particularly highlighted by the MSE estimates, indicating the predictive power of the random forest model.

Table 2: R-squared of the linear regression of fitted vs observed COTS, concordance correlation coefficient (CCC), and mean squared error (MSE) for models R1.0-R2.3 for the zero-inflated negative binomial GLMM and random forest model for the reef scale data models. The random forest model also includes variance explained.

	GLMM			Random forest			
	R-squared	CCC	MSE	R-squared	CCC	MSE	Var Explained
R1.0	0.707	0.708	10.668	0.633	0.761	7.400	63.058%
R1.1	0.717	0.607	14.245	0.633	0.755	7.454	62.791%
R1.2	0.721	0.603	14.359	0.578	0.712	8.594	57.399%
R1.3	0.702	0.592	16.295	0.518	0.641	12.105	50.638%
R2.0	0.703	0.590	13.191	0.609	0.752	6.827	60.927%
R2.1	0.720	0.594	13.011	0.610	0.741	6.867	60.703%
R2.2	0.729	0.592	11.590	0.594	0.731	5.765	59.139%
R2.3	0.725	0.617	14.278	0.528	0.659	9.879	52.034%

Table 3: R-squared of the linear regression of fitted vs observed COTS, concordance correlation coefficient (CCC), and mean squared error (MSE) for models S1.0-S2.3 for the zero-inflated negative binomial GLMM and random forest model. The random forest model also includes variance explained.

	GLMM		
	R-squared	CCC	MSE
S1.0	0.127	0.124	19.025
S1.1	0.159	0.151	20.310
S1.2	0.154	0.144	20.634
S1.3	0.146	0.135	21.134
S2.0	0.178	0.205	15.781
S2.1	0.179	0.203	15.848
S2.2	0.176	0.196	16.081
S2.3	0.172	0.189	16.431

We also fit the zero-inflated negative binomial mixed model to the site-scale data and look at the same metrics as with the reef scale. These values are found in Table 3. As evidenced by the R-squared and CCC values, these models fit the data considerably worse than the reef-scale data. This is likely due to the amount of noise in the RHIS dataset, relative to the respective covariates of interest. We point the reader to the Appendix to examine scatter plots of observed COTS vs. the covariates used. However, despite this fit, some useful information may be obtained from these models, particularly if there is agreement with the reef scale modelling. The S2 models all show relatively similar fit according to all measures.

We examine the model performance from the perspective of the variance explained by considering Nakagawa's R-squared value (Nakagawa, 2017). We specifically calculate the conditional R-squared value which, despite the name, as Nakagawa (2017) notes, is interpreted as the total variance explained by the model. This then helps us determine how informative our model is. We present the results for these values for both reef scale and site scale data GLMMs in Table 4. Critically, we notice that the R-squared values in this table are considerably higher than the predictive R-squared values above, especially for the site scale models. This indicates that the random effects of year and reef ID are critically important in explaining the observed abundance of COTS.

Table 4: Nakagawa's conditional R-squared value for Reef and Site scale data, accounting for random effect and fixed effect variations. M stands for either R or S.

Model	Reef	Site
M1.0	0.700	0.713
M1.1	0.892	0.828
M1.2	0.890	0.823
M1.3	0.927	0.823
M2.0	0.893	0.802
M2.1	0.895	0.810
M2.2	0.901	0.807
M2.3	0.926	0.807

3.2 Reef Scale Models

In this section we present the results of the GLMM and random forest model for the reef-scale data.

3.2.1 Zero-Inflated Negative Binomial Mixed Model Results

Table 5 gives the estimated parameter values as well all their associated p-value for R1 models. In all R1 models, the number of manta tows in an observation was significantly positive. Also, the mean hard coral cover was significantly positive for models R1.1-R1.3, with a nearly significant p-value at 0.05 for R1.0. This suggest that more COTS are observed at sites with higher hard coral cover. Bleaching ASI (average severity index) was only significant in R1.3, when it was the only variable in the model (besides the offset number of manta tows). This gives some indication that bleaching may have some effect, but it clearly is not a primary driver, particularly when hard coral cover is considered.

Regarding results that were not significant, the variable dist_cover was not significant, indicating that higher differences in aggregated hard coral cover was not associated with an effect on the COTS observed. Rubble and macroalgae did not show up as significant in these models. Lastly, outer shelf and latitude were estimated to have a negative relationship, but this was not significant. This indicates that the data does not have the power to detect a significant result in these models, but the parameter estimate supports the idea that COTS were generally observed to be further south in the GBR during the period of this monitoring, and that fewer COTS were observed on the outer shelf reefs.

Table 5: Coefficients (and p-values) for the zero-inflated negative binomial mixed model under formulations R1.0-R1.3. Bold values indicate significance under 0.05. Italicized values indicate significance under 0.10.

Variable	R1.0	R1.1	R1.2	R1.3
log (N)	**0.814 (0.002)**	**0.876 (0.000)**	**0.873 (0.000)**	**0.814 (0.000)**
bleached_ASI	18.606 (0.689)	-7.772 (0.580)	-9.366 (0.481)	**-18.708 (0.015)**
mean_cover	*0.120 (0.051)*	**0.071 (0.004)**	**0.073 (0.003)**	NA
dist_cover	0.058 (0.559)	-0.018 (0.634)	-0.020 (0.600)	NA
rubble	-0.282 (0.351)	-0.079 (0.340)	NA	NA
macroalgae	-0.00621 (0.747)	-0.00478 (0.797)	NA	NA
shelfouter	-3.855 (0.259)	NA	NA	NA
latitude	-0.568 (0.198)	NA	NA	NA

We also present the confidence intervals of each of these variables, shown visually in Figure 2. A critical point is that the uncertainty associated with the bleaching severity index is greater than other variables, although the scale at which bleaching severity is measured is also an order magnitude larger and must be interpreted with that in mind. Though we do not present it here, scaling the variables did not change the results, with bleaching ASI still having a wider range of uncertainty.

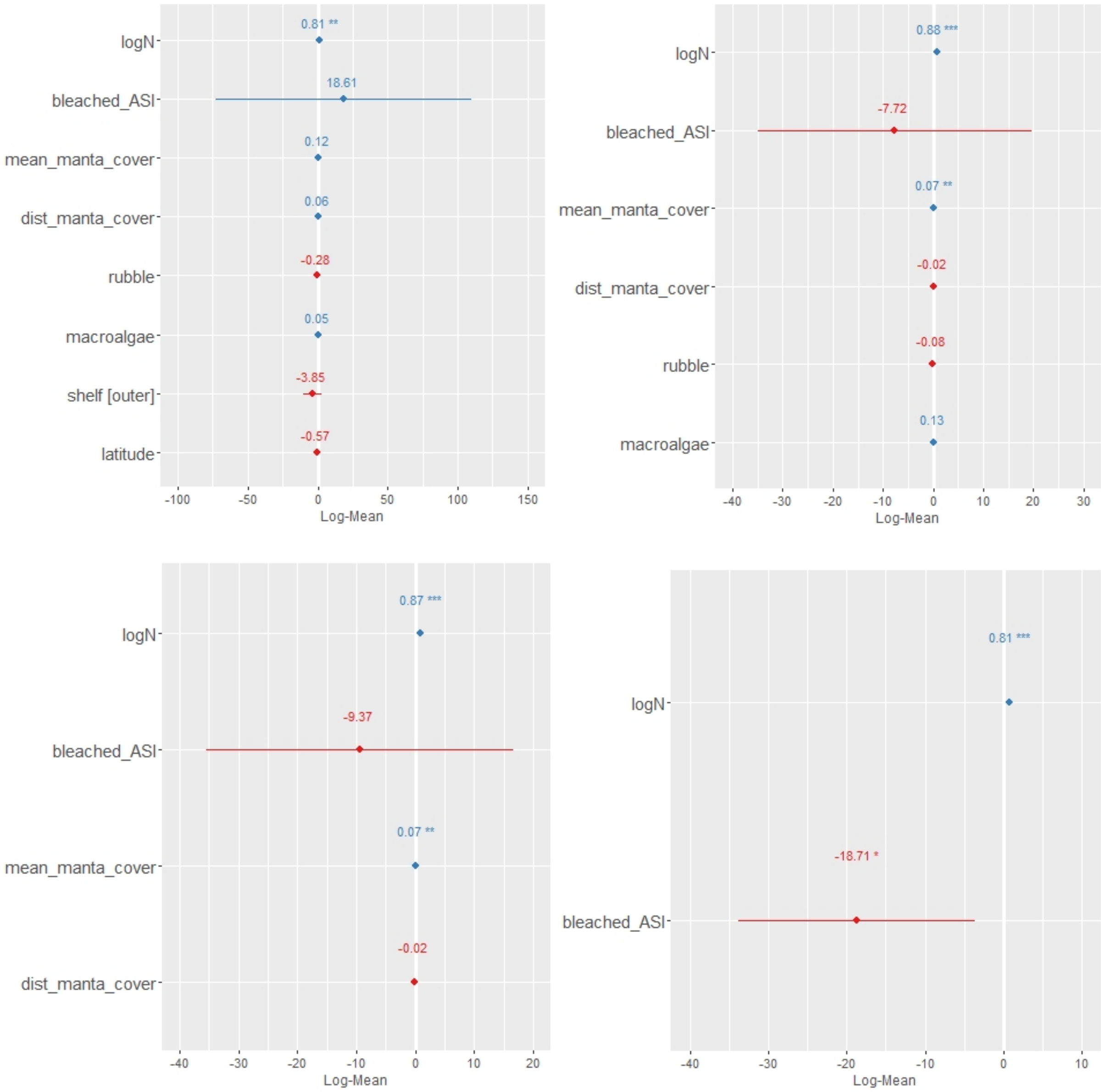


Figure 2: Plot of estimates and confidence intervals using the GLMM for each variable under R1.0 (top left), R1.1 (top right), R1.2 (bottom left), and R1.3 (bottom right). Blue indicates positive values while red indicates negative. Stars (1, 2, or 3) indicate significance under 0.01, 0.05, or 0.1 p-values.

Regarding the GLMM results for the R2 models, parameter estimates, and their associated p-values can be found in Table 6. These results are consistent with the results from the GLMM for R1. We note, however, that only the log(N) variable was significant in all R2 models. Interestingly, the mean hard coral cover only reached significance when it was in the model with the bleaching categorical variables and cover distance only, though it was significant under a threshold of 0.1 for model R2.1. We further note that latitude was significantly negative in R2.0.

Under model R2.2, the mean hard coral cover was significantly positive, while under R2.3, bleaching categories 2, 3, and 4 were significantly negative, with increasingly negative values with increasing category. This indicates that the more severely bleached a reef is, the fewer the COTS observed there. However, the fact that bleaching only becoming significant when it is the only variable included in the model suggests that it is not a key driver of COTS density. We also note that models R2.2 and R2.3 had the best predictive power according to Table 2. This is likely due to the fact that they were fit with more observations (367 and 623, respectively), than R2.0 and R2.1 (233 and 248, respectively). This difference in sample size is due to the large number of observations that were missing the additional covariate data required for models R2.0 and R2.1. Lastly, we present the confidence intervals in Table 6. As with the R1 models, bleaching had the widest confidence interval.

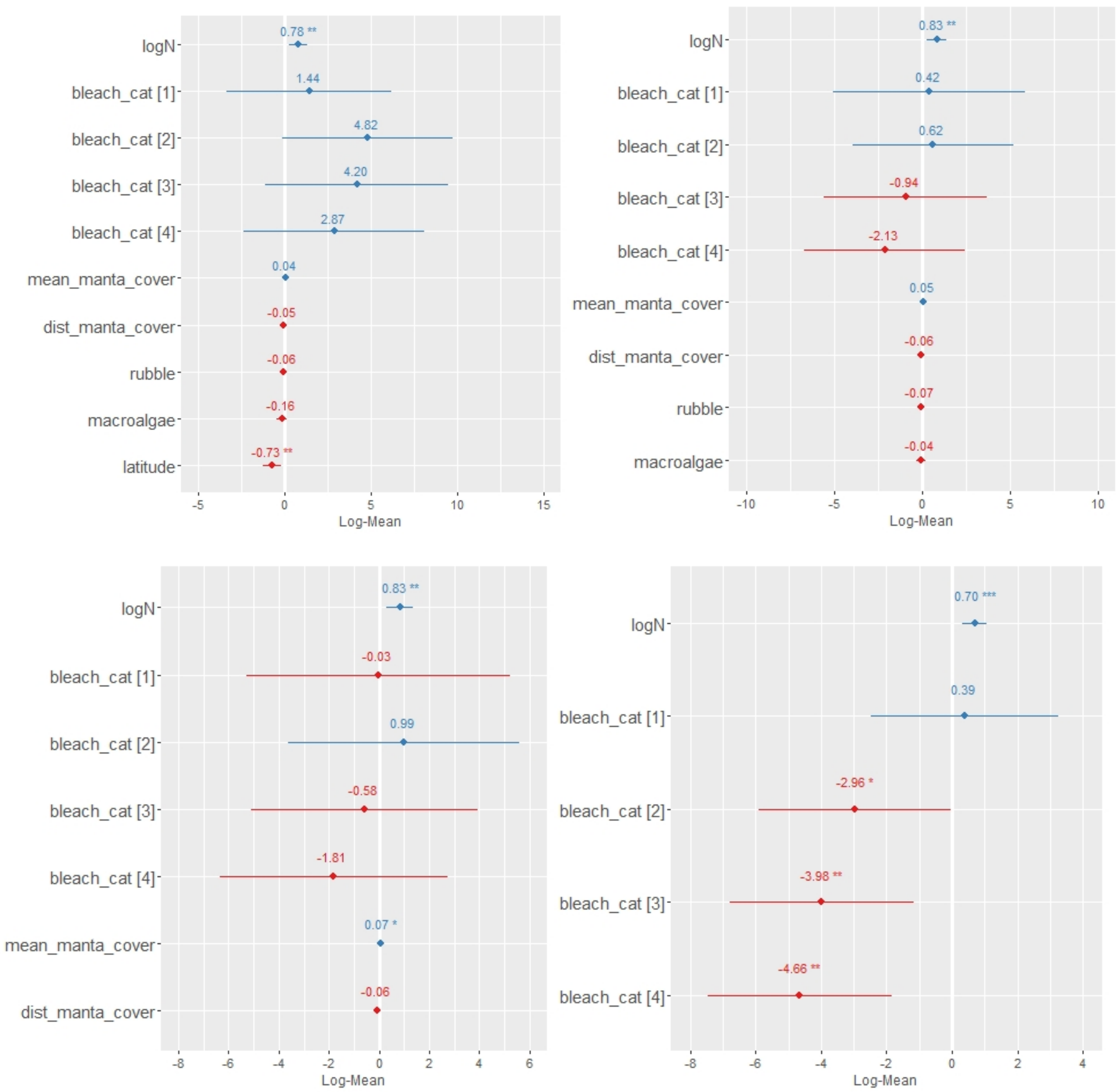


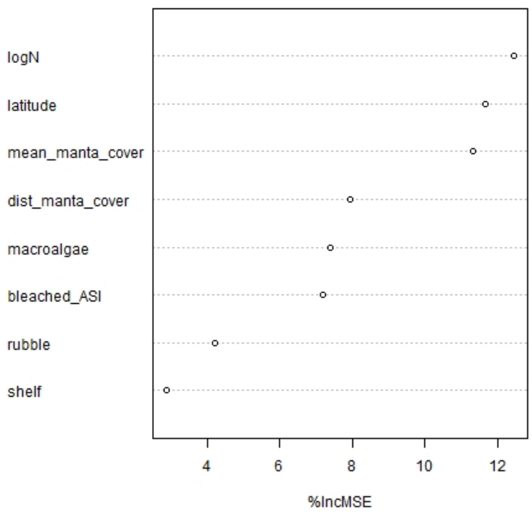
Figure 3: Plot of estimates and confidence intervals using the GLMM for each variable under R2.0 (top left), R2.1 (top right), R2.2 (bottom left), and R2.3 (bottom right). Blue indicates positive values while red indicates negative. Stars (1, 2, or 3) indicate significance under 0.01, 0.05, or 0.1 p-values.

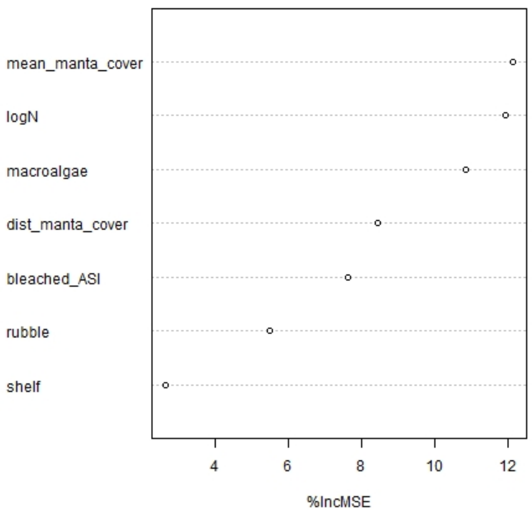
Table 6: Coefficients (and p-values) for the zero-inflated negative binomial mixed model under formulations R2.0-R2.3. Bold values indicate significance under 0.05. Italicized values indicate significance under 0.10.

Variable	R2.0	R2.1	R2.2	R2.3
log (N)	**0.931 (0.001)**	**0.807 (0.005)**	**0.829 (0.002)**	**0.699 (0.000)**
bleach_cat 1	*1.438 (0.555)*	0.416 (0.881)	-0.027 (0.992)	0.386 (0.791)
bleach_cat 2	4.825 (0.056)	0.620 (0.791)	0.991 (0.673)	**-2.962 (0.049)**
bleach_cat 3	4.198 (0.121)	-0.940 (0.692)	-0.579 (0.802)	**-3.980 (0.005)**
bleach_cat 4	2.871 (0.281)	-2.131 (0.363)	-1.806 (0.436)	**-4.659 (0.001)**
mean_cover	0.0430 (0.139)	*0.043 (0.070)*	**0.067 (0.019)**	NA
dist_cover	-0.047 (0.270)	-0.057 (0.183)	-0.060 (0.149)	NA
rubble	-0.060 (0.473)	0.0124 (0.408)	NA	NA
macroalgae	-0.160 (0.263)	-0.040 (0.771)	NA	NA
latitude	-**0.734 (0.006)**	NA	NA	NA

3.2.2 Random Forest Results

The nature of the random forest algorithm allows for interactions between variables (see Breimann, 2001 for details). These variables can be ranked by a measure of importance. Such a measure accounts for how much the mean squared error is reduced when each variable is included in building an individual tree in the forest. To give an indication of what variables are helpful in determining the location of COTS observations, we therefore present this importance measure, reported as percent increase in mean squared error (%IncMSE) when that variable is not included. A higher value indicates that variable is more important. Figure 4 show the results for the R1 models while Figure 5 show the results for the R2 models. For the R1 models, log(N) was the most important variable in all models except R1.1. Latitude and mean hard coral cover also showed similarly high importance. Interestingly, the distance hard coral cover variable also showed importance in predicting observed COTS, generally near the same importance as macroalgae and bleached ASI. Critically, these results generally agree with the GLMM models, indicating that hard coral cover is a critical variable in explaining COTS observations, while also including the potential spatial variable in latitude as an important predictor.





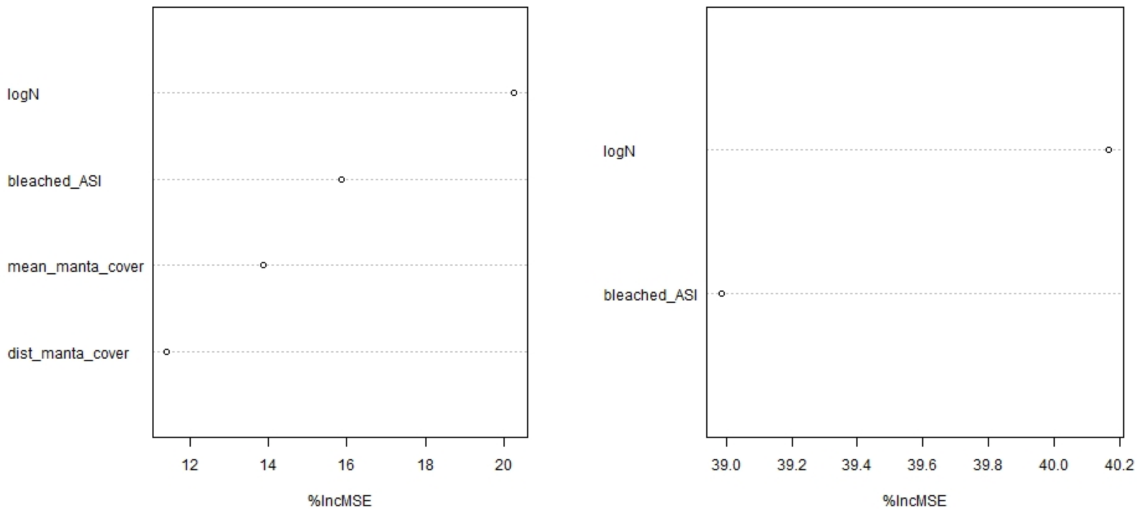


Figure 4: Variable importance rankings for the random forest implementation using R1.0 (top left), R1.1 (top right), R1.2 (bottom left), and R1.3 (bottom right).

The R2 model results showed less consistent results, highlighting the potential of rubble as an important predictor of observed COTS. Bleaching category did show high importance, but hard coral cover also showed potential importance. Latitude, however, was the primary predictor, indicating that spatial location is a primary driving factor in predicting observed COTS.

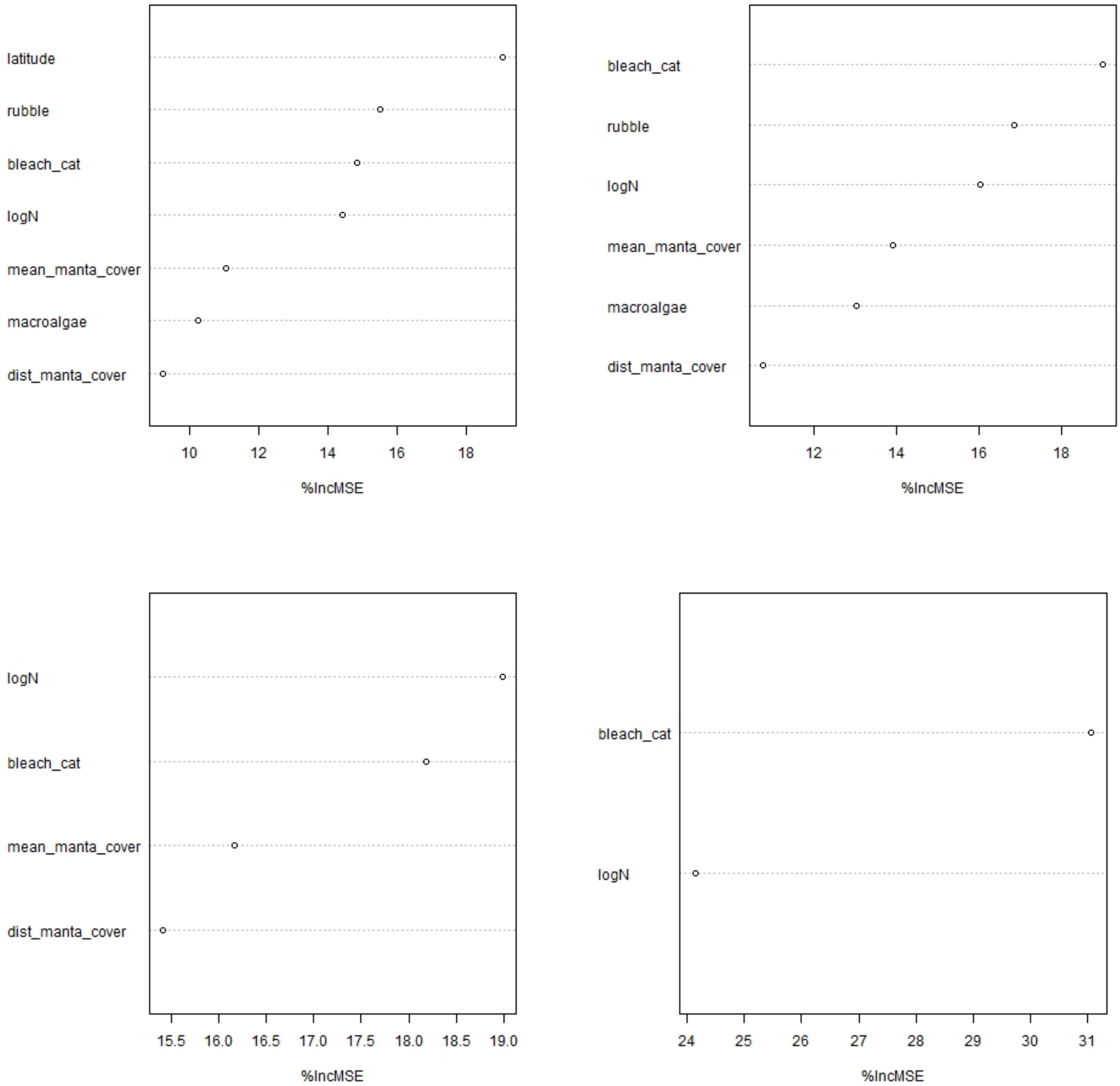


Figure 5: Variable importance rankings for the random forest implementation using R2.0 (top left), R2.1 (top right), R2.2 (bottom left), and R2.3 (bottom right).

3.3 Site Scale Models

In this section we present the results of the GLMM for the site-scale data.

Table 7 gives the estimated covariate parameter values and associated p-values for S1 models described in Section 2.4. Coral cover was significantly positive in all S1 models, agreeing with the reef scale models, indicating that more COTS were observed at higher coral cover percentages. Bleached ASI was significant for S1.1-S1.3 models, without the inclusion of latitude or shelf. Latitude was also significantly negative in S1.0. Rubble was significantly positive as well, indicating that higher proportions of rubble are associated with more observed COTS. This did not show up in reef scale results, but given the finer scale, rubble likely has some influence on COTS abundance.

Regarding habitat and aspect, which are only in the site scale models, S1.0 showed significance for increased observed COTS at lagoon and slope habitats relative to crest. S1.1 showed the same as well as increased COTS observed at reef flat habitats, and an increase in observed COTS on sites with a southeast and southwest aspect, relative to those with a northeast aspect.

Confidence intervals of each variable are shown in Figure 6. Because of larger sample sizes in the site-based models, the confidence intervals tend to be narrower than those in the reef-scale models. This explains why the bleaching ASI interval is narrower than in the reef-based models. However, it also gives some indication that we have more confidence in the significance in bleaching ASI. This must be considered in light of the fact that these models overall fit to the data is worse, as well as noting that hard coral cover is still significant and likely confounded with bleaching ASI.

Table 7: Coefficients (and p-values) for the zero-inflated negative binomial mixed model under formulations S1.0-S1.3. Bold values indicate significance under 0.05. Italicized values indicate significance under 0.10.

Variable	S1.0	S1.1	S1.2	S1.3
bleached_ASI	0.032 (0.894)	**-0.490 (0.000)**	**-0.462 (0.000)**	**-0.346 (0.000)**
coral_cover	**0.026 (0.000)**	**0.023 (0.000)**	**0.021 (0.000)**	NA
macroalgae	0.011 (0.134)	0.002 (0.423)	NA	NA
rubble	*0.010 (0.081)*	**0.007 (0.000)**	NA	NA
habitat Lagoon	**0.751 (0.000)**	**0.268 (0.000)**	NA	NA
habitat Reef flat	-0.278 (0.313)	**0.203 (0.003)**	NA	NA
habitat Slope	**0.477 (0.048)**	**0.161 (0.039)**	NA	NA
aspectNW	0.029 (0.878)	-0.113 (0.112)	NA	NA
aspectSE	*-0.455 (0.086)*	**0.268 (0.002)**	NA	NA
aspectSW	-0.146 (0.492)	**0.214 (0.001)**	NA	NA
shelfouter	-1.236 (0.257)	NA	NA	NA
latitude	**-0.362 (0.030)**	NA	NA	NA

Table 8: Coefficients (and p-values) for the zero-inflated negative binomial mixed model under formulations S2.0-S2.3. Bold values indicate significance under 0.05. Italicized values indicate significance under 0.10.

Variable	S2.0	S2.1	S2.2	S2.3
bleach_cat 1	0.853 (0.492)	0.387 (0.759)	0.269 (0.827)	0.346 (0.778)
bleach_cat 2	0.372 (0.804)	-1.451 (0.251)	-1.584 (0.199)	-1.591 (0.196)
bleach_cat 3	0.501 (0.742)	-1.459 (0.236)	-1.561 (0.192)	-1.669 (0.162)
bleach_cat 4	-0.720 (0.643)	-2.757 (0.026)	**-2.872 (0.017)**	**-3.002 (0.012)**
coral_cover	**0.022 (0.000)**	**0.022 (0.000)**	**0.020 (0.000)**	NA
macroalgae	0.006 (0.174)	0.006 (0.164)	NA	NA
rubble	0.001 (0.818)	0.001 (0.843)	NA	NA
habitat Lagoon	0.071 (0.543)	0.066 (0.572)	NA	NA
habitat Reef flat	0.186 (0.189)	0.176 (0.212)	NA	NA
habitat Slope	-0.180 (0.267)	-0.167 (0.300)	NA	NA
aspectNW	0.142 (0.260)	0.143 (0.257)	NA	NA
aspectSE	**0.373 (0.012)**	**0.381 (0.010)**	NA	NA
aspectSW	**0.239 (0.047)**	**0.248 (0.039)**	NA	NA
latitude	**-0.346 (0.043)**	NA	NA	NA

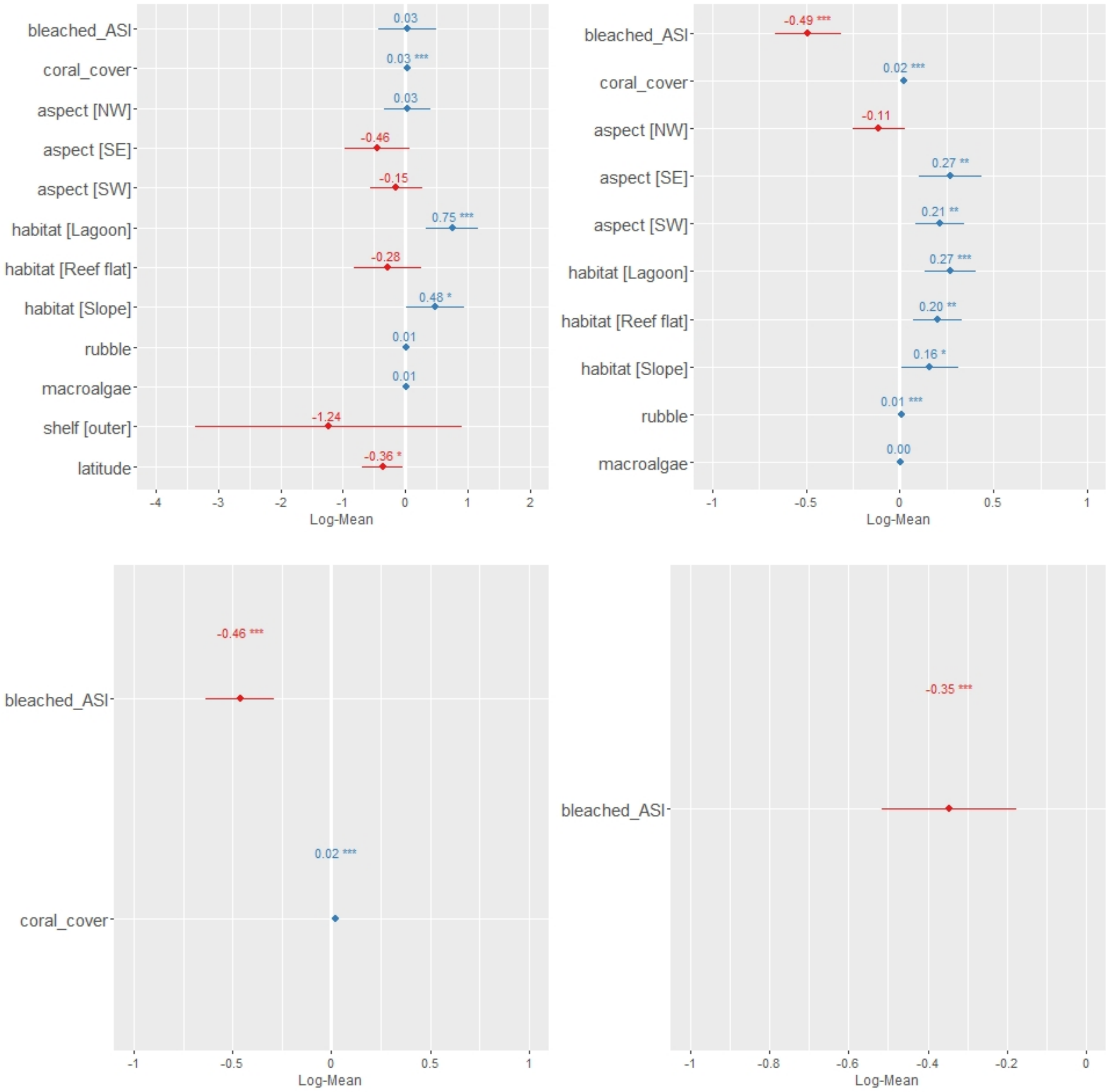


Figure 6: Plot of estimates and confidence intervals using the GLMM for each variable under S1.0 (top left), S1.1 (top right), S1.2 (bottom left), and S1.3 (bottom right). Blue indicates positive values while red indicates negative. Stars (1, 2, or 3) indicate significance under 0.01, 0.05, or 0.1 p-values.

Table 8 shows the results for the S2.0-S2.3 models, giving estimates of the parameters and their associated p-values. Latitude was again significantly negative, agreeing with the reef-scale models and S1 models. Coral cover was also significantly positive in all models, agreeing with the previous results as well. Aspect showed significance for sites with southwest and southeast aspects, agreeing with S1 models. However, sites with a northwest aspect were not significant, unlike in S1.1. Rubble was not significant in S2 models unlike S1 models. Bleaching category only became significant and only in category 4 when considering S1.2 and S1.3. However, this generally agrees with the reef-scale models in which bleaching category only was for model R2.3. The difference being that category 4 in this case (the most severely bleached coral category) was significantly negative when observing COTS. Figure 7 shows the confidence intervals for S2.0-S2.3 models.

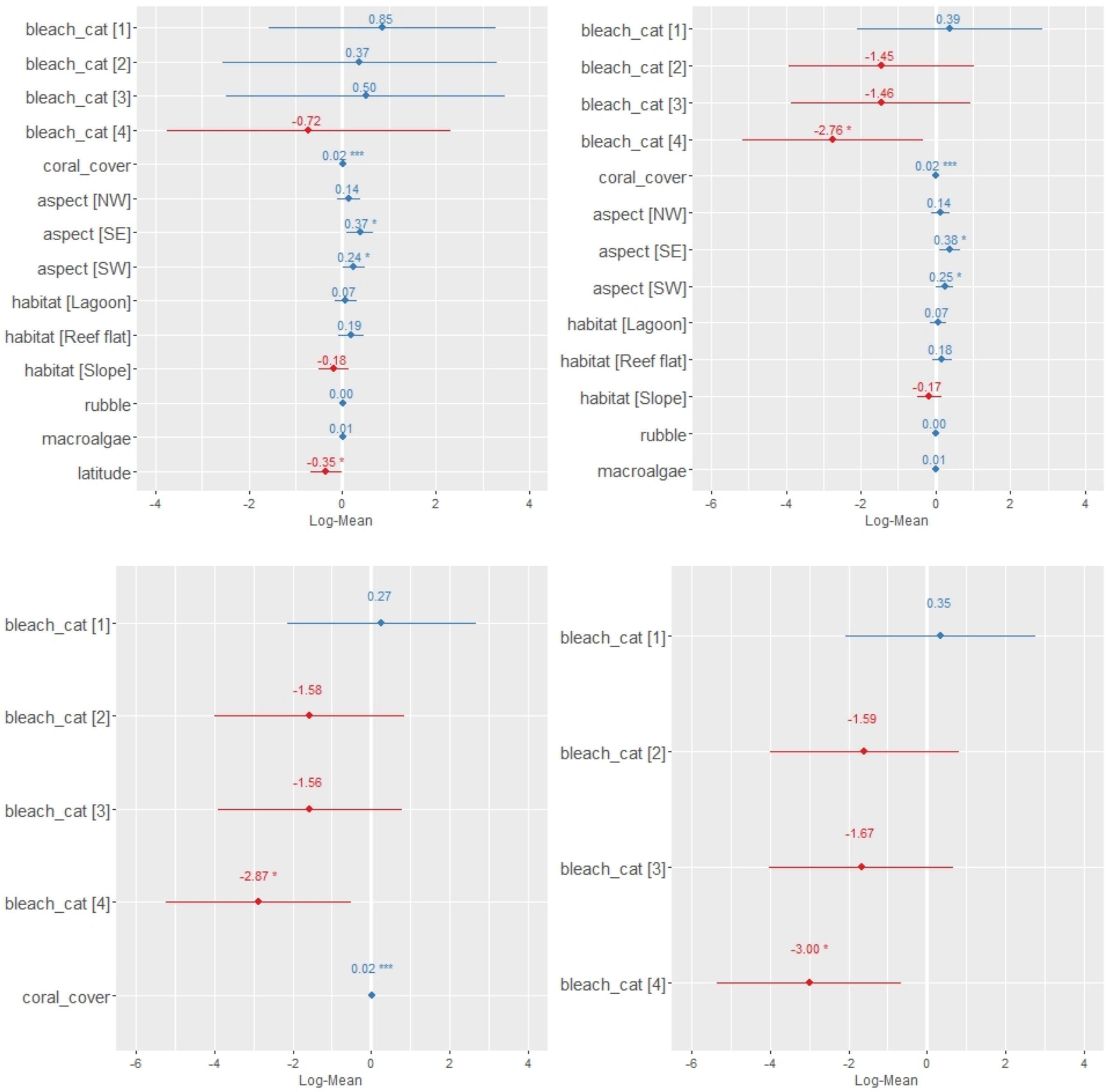


Figure 7: Plot of estimates and confidence intervals using the GLMM for each variable under S2.0 (top left), S2.1 (top right), S2.2 (bottom left), and S2.3 (bottom right). Blue indicates positive values while red indicates negative. Stars (1, 2, or 3) indicate significance under 0.01, 0.05, or 0.1 p-values.

While the site based models do show some environmental and spatial variables that are significant in the observation of COTS, it is important to take into account the goodness of fit of these models, as noted from. This suggests that the primary drivers are still the random effect variables, specifically the year and Reef ID, while the specific fixed effects should be taken as a signal given the random effects.

4.0 DISCUSSION

Implementing effective management interventions to protect coral cover against the cumulative effects of bleaching and COTS predation on the GBR requires a good understanding of the spatial and temporal distribution of each impact, as well as interactions between them. The results of this analysis show that environmental, spatial, and temporal factors influence the observation of COTS on the GBR. COTS density shows only a weak negative response to the presence of bleached coral, suggesting that bleaching is not a major determinant of observed COTS abundance. In contrast, the overall percentage of hard coral cover was positively related to COTS abundance. This is an unsurprising result, given hard coral is the preferred food source for COTS. However, it provides an important insight for management: effort should be targeted at reefs and reef sites with high hard coral cover, independent of their bleaching history.

We implemented a generalized linear mixed model and a random forest model to reef-scale data, and a generalized linear mixed model to site scale data, to determine what environmental factors influence the abundance of COTS on reefs on the GBR. We developed these models with an explicit focus on the effects of hard coral cover and coral reef bleaching. A critical question was if any identified effect of hard coral cover interacted with effects of bleaching to further influence the abundance of COTS. Utilizing both a negative binomial GLMM and random forest gives key insight into the significant relationships between COTS and the environment, and in prediction of where COTS are likely to be found.

These models control for reef and year by including them as random effects in the model for the GLMM. This is critical as COTS abundance varies widely based on location and year as an outbreak ‘wave’ moves south along the reef over time (Vanhatalo et al., 2016). Consequently, incorporating reef and year as random factors accounts for the distribution of the outbreak over the period during which data was collected.

4.1 Hard Coral Cover

Critically, this study confirms that the observed abundance of COTS is positively related to hard coral cover. For example, the R1.1 model with an estimate of 0.07 for hard coral cover translates to an increase in observed COTS by exp(0.07) = 1.072. In practical terms, this means a 10.9% increase in hard coral cover approximately doubles the number of COTS observed at the reef-scale. For the S1.2 model, with an estimate of 0.02, this means a 44.6% increase in hard coral cover approximately doubles the number of COTS observed at the site scale. It is critical, however, to interpret these results in the context that they are conditional on the random effects of reef ID and year. This is highlighted by the fact that the predictive fits described in Table 2 and Table 3 are relatively low in predictive power, but when the random effects (reef and year) are included (Table 4) the variance explained jumps up significantly. In other words, the dominant factors influencing COTS densities are the spatial location and time relative to the position of the outbreak front, and then, having taken these into account, hard coral cover becomes important.

It is unsurprising that hard coral cover had a significantly positive effect on COTS density in these models, given that hard coral is COTS’ preferred and primary food source. Additionally, however, the data exhibited a bias in that high coral cover was primarily recorded in the newly outbreaking areas. This probably reflects two factors: 1) areas through which the outbreak had already propagated had had hard coral reduced by COTS predation; and 2) data was preferentially collected up to the southern extent of the outbreak. These two effects mean that, in any given year, the highest recorded density of coral coincided with the highest recorded density of COTS.

4.2 Effects of Bleaching

We looked at the effects of bleaching on observed COTS abundance under two scenarios: (1) current bleaching through the average severity index (e.g. R1 and S1 models) and (2) lagged effects of bleaching through bleaching category severity on subsequent near-term years (e.g. R2 and S2 models). In general, observed abundance of COTS is negatively related to the extent of bleaching, particularly in the case of more severe bleaching. However, this is generally only the case when bleaching is the only variable in the model at the reef scale (e.g. R1.3, R2.3) or when there are no other additional spatial variables at the site scale (e.g. S1.2, S1.3, S2.2, and S2.3). The only exception to this was S1.1, in which bleaching ASI was negatively significant with aspect and habitat still in the model (but not with latitude or shelf position).

There is little evidence in the analysis to indicate that COTS are targeting unbleached coral on the reef. Instead, our analysis suggests that they are observed to be more abundant in areas with high hard coral cover. If we assume that bleaching is not uniform across a reef then we would expect that bleaching increases the variability in coral cover at a reef and, that if COTS responded to this variability by moving to locations with higher live coral cover, that there would be a positive relationship between COTS abundance and the variability of coral cover at a reef. In the reef-scale models, variability in hard coral cover (i.e. the "distance" measure of hard coral cover) was not significant in any model. This suggests that within a reef, increased variability in hard coral cover did not result in observation of more COTS. This, combined with the fact that bleaching was only significant when all other variables were removed from the model, provides little evidence to support the claim that COTS are targeting unbleached coral when bleaching is present.

In general, we note that while there is evidence that the magnitude of bleaching has a significant and negative influence on the observed abundance of COTS at both reef and site scales, that effect only becomes apparent when other factors are excluded. This suggests that the most influential factor in determining observed COTS abundance is hard coral cover and not bleaching.

4.3 Environmental and Spatial Factors

Latitude tended to be significantly negative in each model, indicating that samples collected further south reported higher COTS numbers. The negative sign of this relationship is an artefact of sampling, in that during the time data was collected, the COTS outbreak happened to be located in the southern part of the sampled area. This signal is augmented by the ongoing outbreak occurring in the Swains, a cluster of reefs in the far south that drive a small negative response with latitude, independent of the main outbreak further north. More importantly, however, the strength of the significance of the relationship with latitude indicates that outbreaking reefs tend to be clustered along a latitudinal band at the southern end of the sampled region. The fact that the relationship between COTS count and latitude shows significance where other variables included in the model do not is indicative that this clustering of high COTS counts around the outbreak front is a stronger signal than the environmental factors considered. In terms of management, this suggests it is more important to focus control effort on where the outbreak is located than responding to other environmental factors.

In the site-based models we found that when aspect and habitat are included, observed COTS abundance tended to be higher on the southern aspects of individual reefs, relative to the north-eastern aspect. Model S1.0 showed significantly increased observed COTS for slope and lagoon habitats, relative to crest; this suggests that COTS prefer less wave action. This was further confirmed by the fact that the outer shelf tended to be negative in observed COTS, noting that COTS would prefer regions of the GBR less exposed to open ocean influences.

Rubble had a significant and positive effect but only in the site-scale models. This may reflect differential patterns of local recruitment to a site. Crustose coraline algae forms on rubble and is considered to be the preferred settlement substrate for larvae (e.g. Fabricius and De'ath, 2001; Wilmes et al, 2017) and the preferred diet of juveniles <10mm diameter (Pratchett et al. 2014; Deaker et al., 2020). This might suggest that, with incomplete redistribution of >10mm diameter COTS across a reef, sites with, or close to, areas of rubble might be expected to have higher adult COTS densities. Importantly, we note that rubble was a fixed effect, and as evidenced by the model performance indicators, the fixed effects have a smaller driving effect on the observation of COTS than the effects for reef and year.

4.4 Data Limitations

A key issue in seeking to answer the questions considered by this study is the availability of data relative to the variance of the data collected. RHIS data is accurate and precise over the sampled area but covers a small proportion of any given reef. Manta tow data covers larger areas but is both less accurate and less precise. Extracting a clear reef-scale signal requires, ideally, accurate data over the scale of a reef, which the limitations of our sampling methods struggle to provide. At the site scale, RHIS data provides accuracy and precision, but the significant variation in COTS densities across sites on reefs on the GBR require a proportionally larger sample size to produce statistically significant results, as discussed further below.

An obvious concern is the consistency of data fused from multiple monitoring programs. However, the widespread use and standardised protocols for both RHIS and manta tow means there is likely to be reasonable consistency across the monitoring programs from which data was collated. Observers are well trained to the same standard across programs, and so there is no reason to suspect bias between monitoring programs for either sample type. Additionally, different data sources are used for different analyses, with the site-based models being based on the RHIS datasets while the reef-based analysis is based on both manta tow surveys and an aggregation across RHIS sites. Given this, the fact that the reef-scale and site-scale analyses agree should strengthen our confidence in the results.

An added complication was the need to model COTS at high spatial resolution for the site-scale analysis. At this resolution the data is extremely noisy, as evidence by the scatterplots presented in the Appendix. Though our method does account for variability across time (years) and within a specific reef (spatial), some variables that were of interest are simply too variable to extract any signal. Our analysis carefully weighed the benefit of aggregating to the reef scale to gain a more robust dataset, versus retaining information at the site scale in order to infer COTS habitat preferences. Given a critical question of this study was how observed COTS abundance was influenced by bleached or non-bleached coral in relation to the available percentage of hard coral cover, it was important for us to focus part of the analysis at the site level, which subsequently revealed a strong correlation between increasing bleaching category and decreasing hard coral cover.

This also raises a very important question: how reliable are these results? This question must be taken in the context of the overall performance of the models. While total model performance, i.e. including random factors, was high (0.7-0.926; Table 4) the predictive performance was lower (0.127-0.729, Tables 2 and 3). Given the observed variability in the datasets, significant model improvements are unlikely without sampling targeted specifically at answering the questions being considered.

Nevertheless, the observation that the variation in COTS abundance in our models is attributed more to random effects, specifically that of reef and year, highlights that COTS tend to be distributed at certain outbreaking reefs that tend to be distributed along an outbreak front at a specific latitude at a specific point in time. Fixed effects, specifically hard coral cover at a reef, are a secondary driver of COTS densities. Bleached reefs have at most a small negative impact on observed COTS densities.

The relevance of these results to more effective targeting of management efforts for COTS on the GBR is that COTS densities are primarily determined by the overall stage of the outbreak in a region, and the hard coral cover at a specific reef. Further improving our understanding of the location of high densities of COTS within an individual reef would require additional or higher quality data. The amount of additional data would be required to identify these trends could be estimated using a power analysis.

4.5 Conclusions

Leveraging the best data currently available across a range of monitoring and control programs on the GBR, we have shown that high densities of COTS are most likely to be found near the latitude of the outbreak front, on reefs with high coral cover. This is a significant result, because it highlights the importance of targeting control efforts in these areas, as is currently being done by the national COTS Control Program. Vitally, this result holds even for data collected during and following the major back-to-back bleaching events in 2016/2017 on the GBR. This suggests that even during such an event, managers should continue to target efforts at reefs near the outbreak front with high coral cover, rather than changing priorities to target reefs that have experienced significant bleaching.

During and immediately following major bleaching, this analysis found no significant relationship between where bleaching occurred and where COTS densities were highest. Over the longer term, reefs that suffered significant coral losses due to bleaching were likely to exhibit both lower hard coral cover and lower COTS numbers, making control there both less effective at protecting coral cover, and less efficient at removing COTS. Crucially, in any scenario, managers need only consider the existing hard coral cover at a reef, which is easily observed, rather than previous bleaching history, which may be less apparent, in order to prioritise reefs for management.

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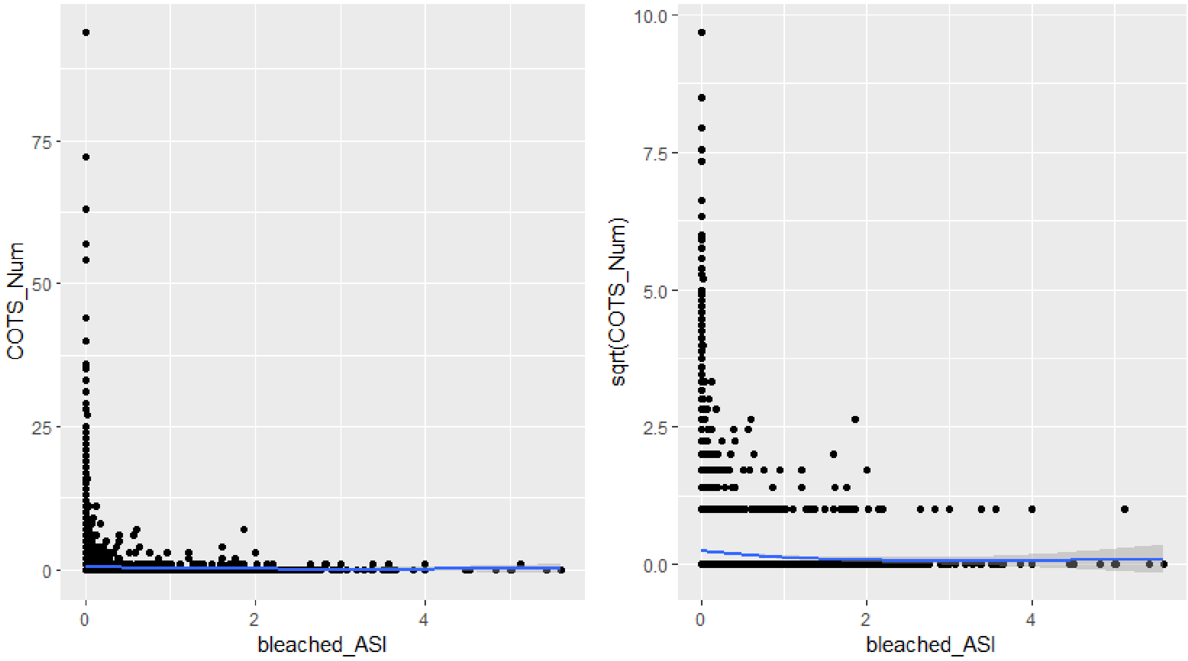
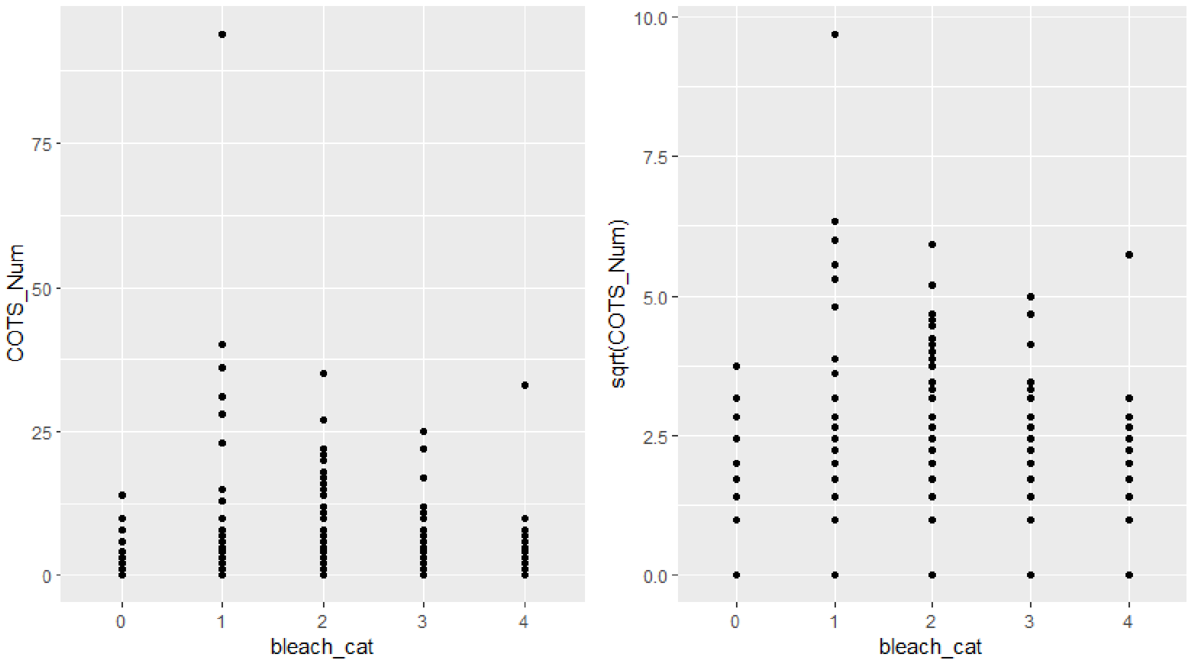
APPENDIX 1: SITE BASED DATA SCATTERPLOTS

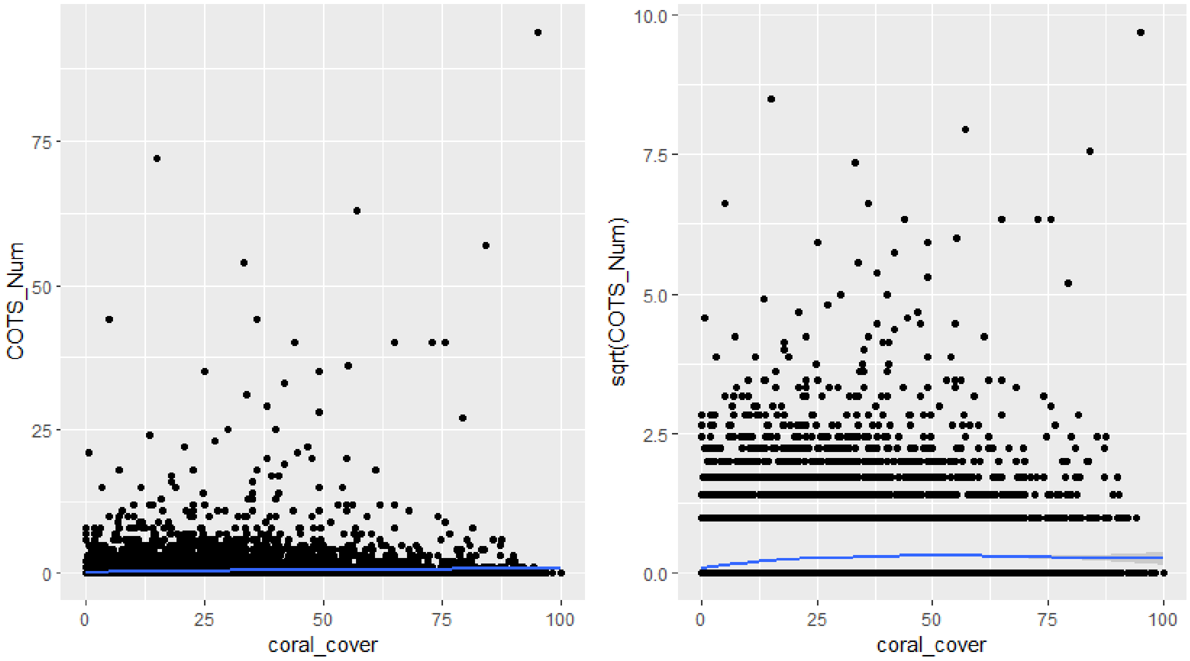
In this appendix, we present scatterplots of the observed COTS counts against the covariates used for the site-based modelling, which come primarily from the RHIS dataset. We plot COTS on the natural scale (left plots) and the square root of observed COTS (right plots).



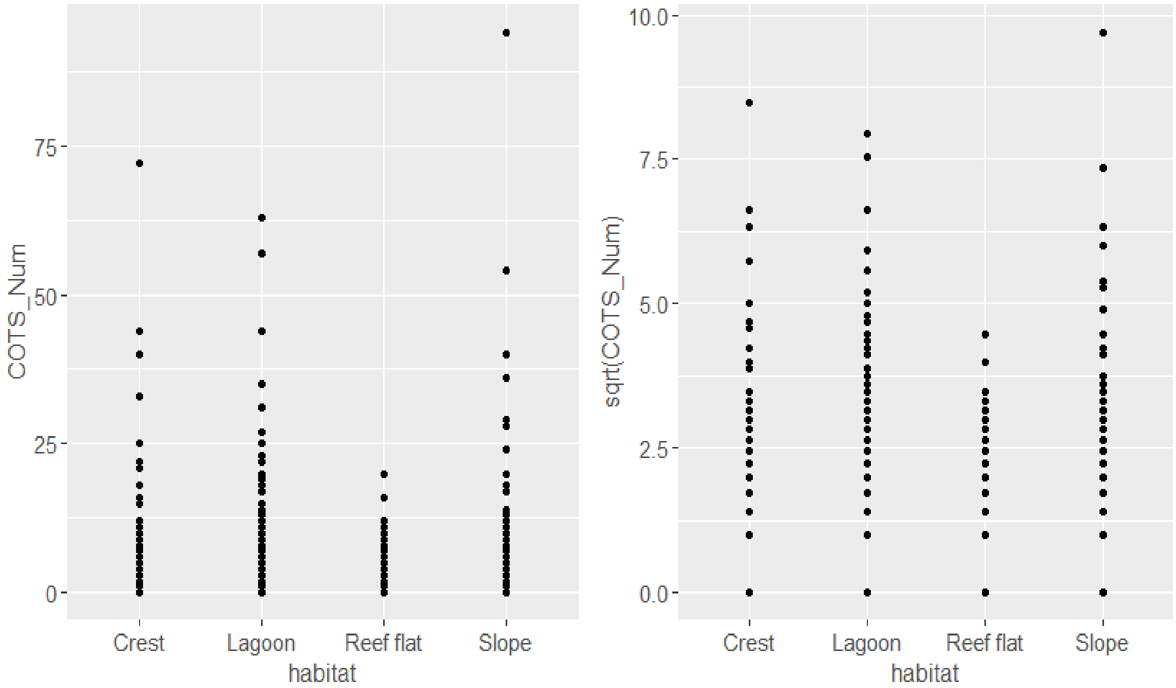
Appendix Figure 1: Scatter plot of COTS observed (left) and square root of COTS observed (right) against Bleached ASI from the site based RHIS data. Blue line indicates a spline smooth fit.



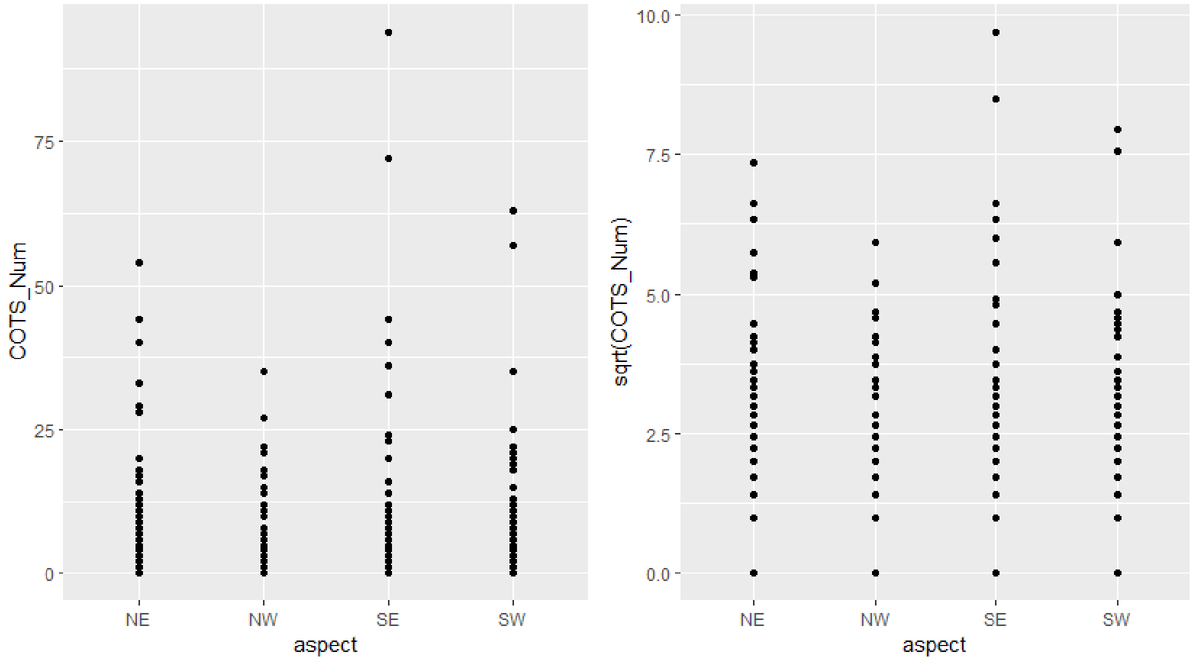
Appendix Figure 2: Scatter plot of COTS observed (left) and square root of COTS observed (right) against Bleached category from the site based RHIS data.



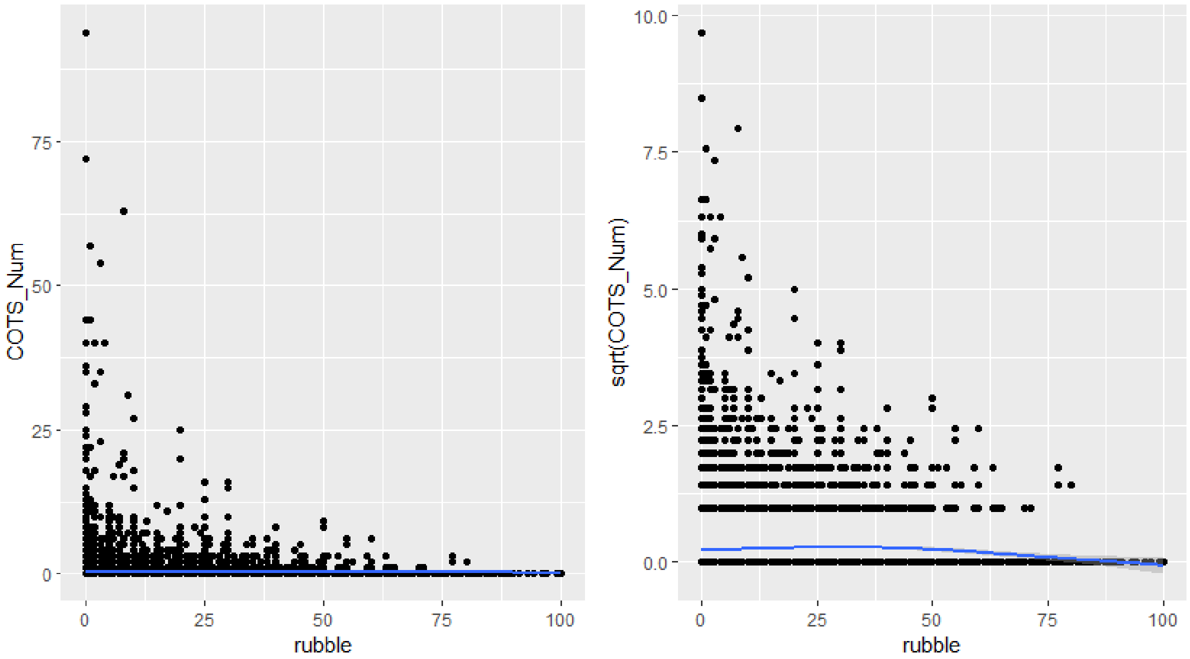
Appendix Figure 3: Scatter plot of COTS observed (left) and square root of COTS observed (right) against coral cover percentage from the site based RHIS data. Blue line indicates a spline smooth fit.



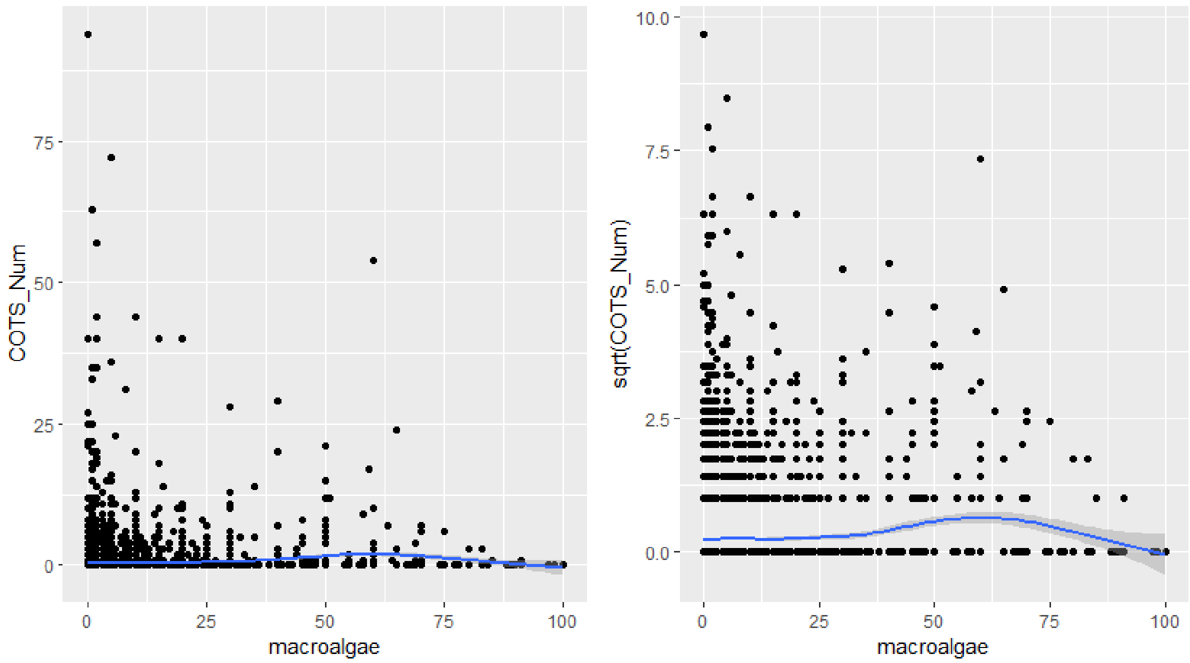
Appendix Figure 4: Scatter plot of COTS observed (left) and square root of COTS observed (right) against habitat from the site based RHIS data.



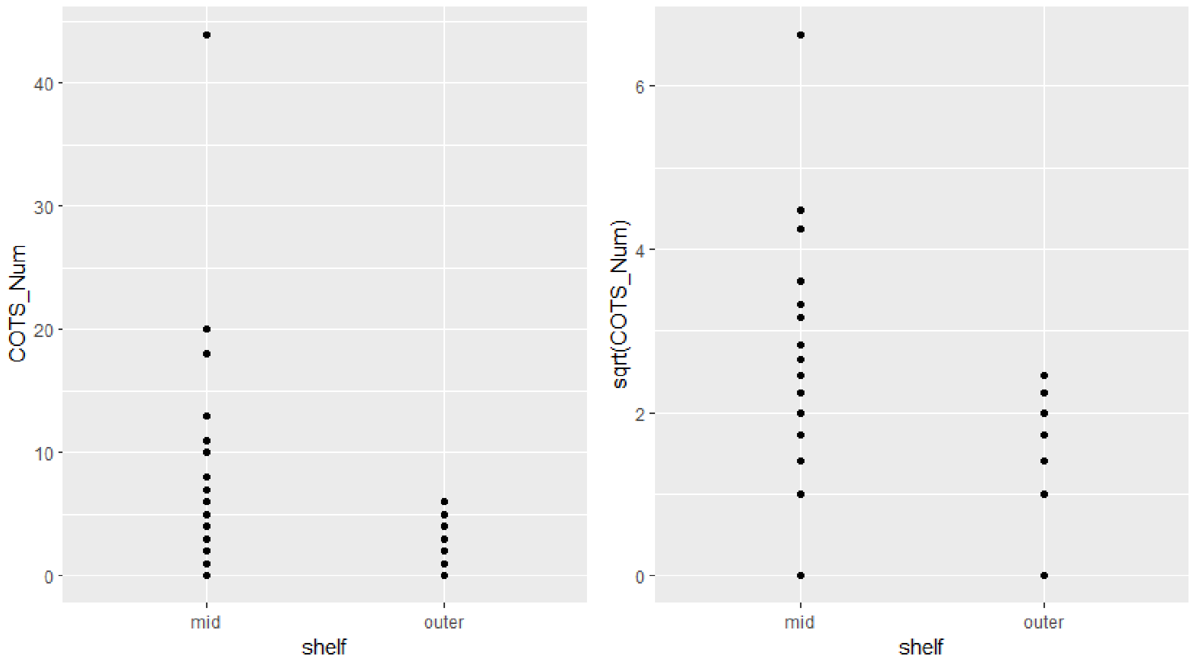
Appendix Figure 5: Scatter plot of COTS observed (left) and square root of COTS observed (right) against aspect from the site based RHIS data.



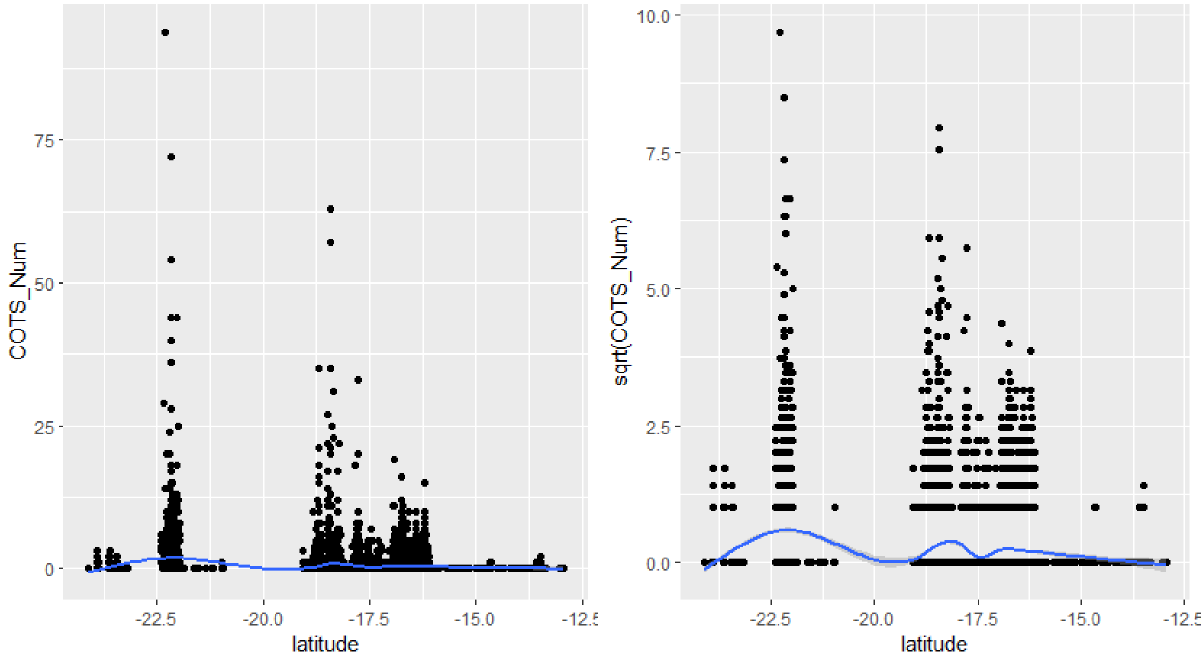
Appendix Figure 6: Scatter plot of COTS observed (left) and square root of COTS observed (right) against rubble from the site based RHIS data. Blue line indicates a spline smooth fit.



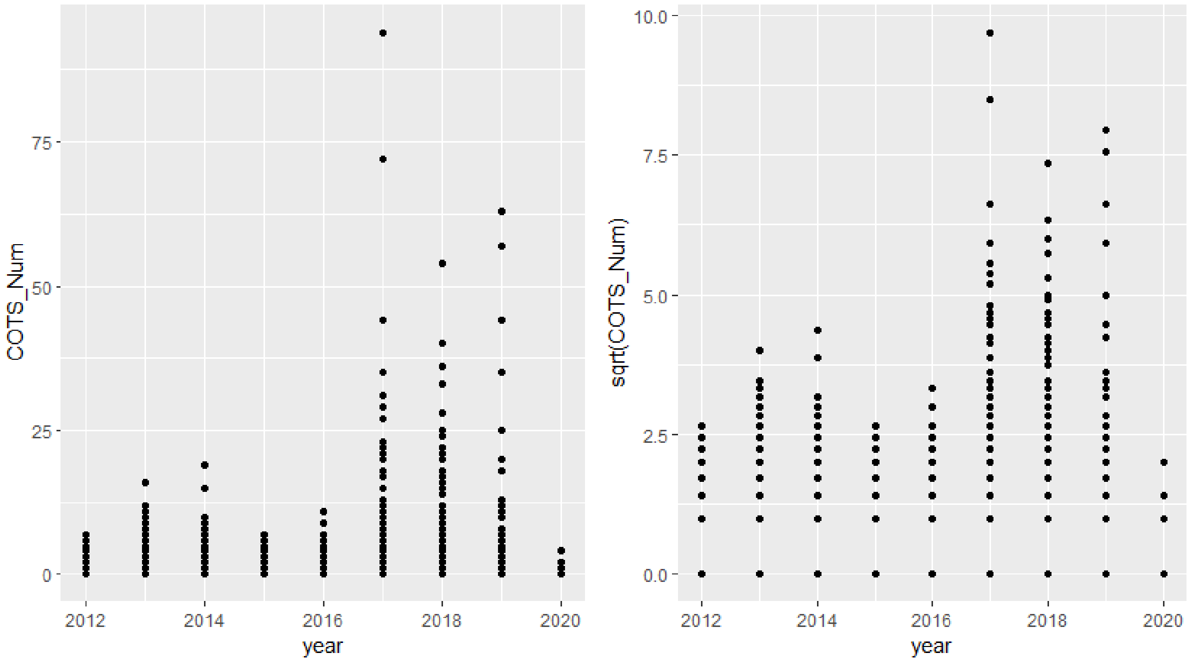
Appendix Figure 7: Scatter plot of COTS observed (left) and square root of COTS observed (right) against macroalgae from the site based RHIS data. Blue line indicates a spline smooth fit.



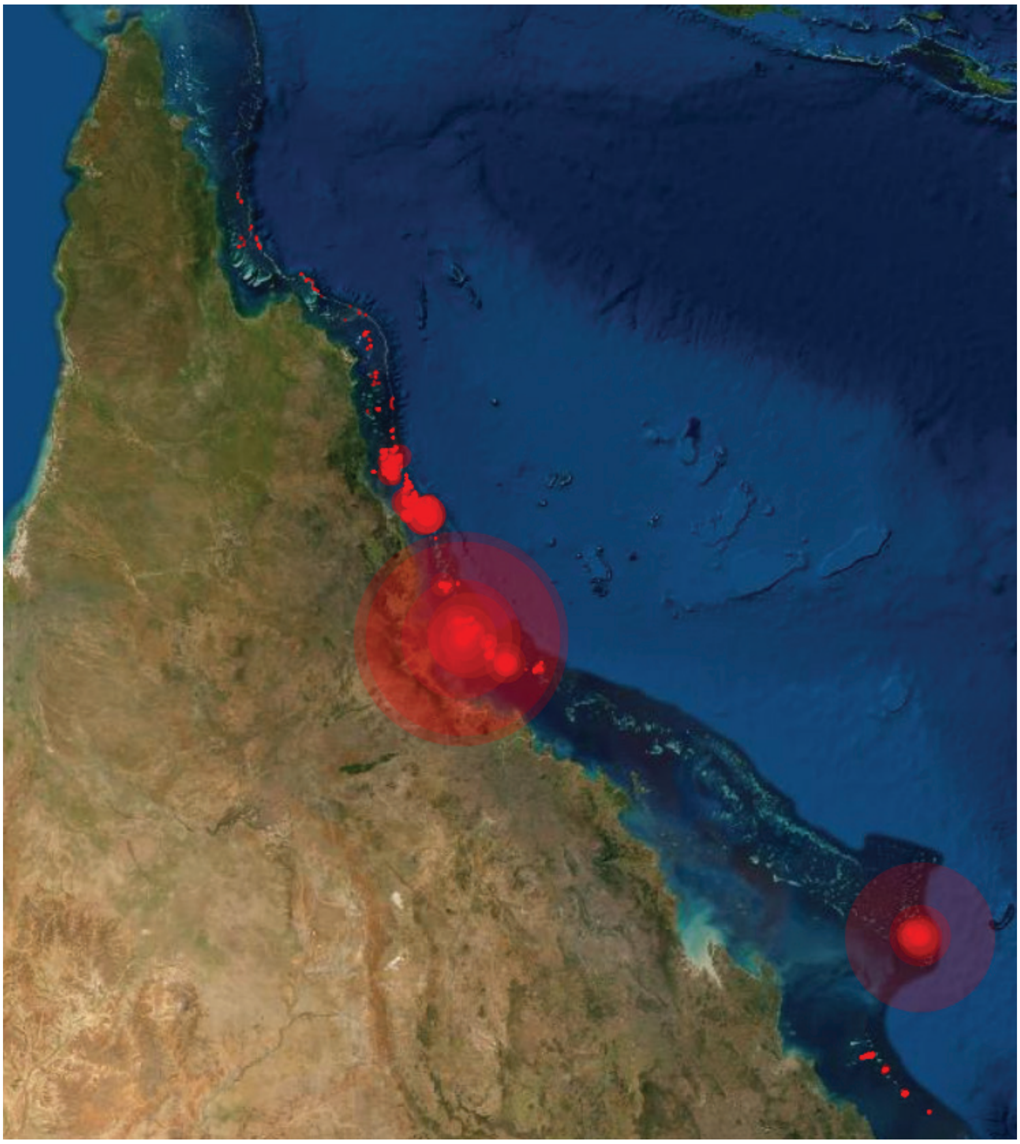
Appendix Figure 8: Scatter plot of COTS observed (left) and square root of COTS observed (right) against shelf from the site based RHIS data.



Appendix Figure 9: Scatter plot of COTS observed (left) and square root of COTS observed (right) against latitude from the site based RHIS data. Blue line indicates a spline smooth fit.



Appendix Figure 10: Scatter plot of COTS observed (left) and square root of COTS observed (right) against year from the site based RHIS data.



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