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Technical Report

Coral Bleaching and Mortality on the Great Barrier Reef

A Data Driven Modelling Approach

Daniel W. Gladish, Scott Condie, Cameron S. Fletcher and David A. Westcott

CSIRO

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Cover photographs: (front) Healthy plate corals on the central GBR. Image David Westcott. (back) Recently dead coral on the central GBR. Image: David Westcott.

This report is available for download from the NESP Tropical Water Quality Hub website:
http://www.nesptropical.edu.au

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ACRONYMS

CI .... Confidence interval
COTS............ Crown-of-Thorns Starfish
CRW .... Coral Reef Watch
EotR.............. Eye on the Reef
FMP .... Field Management Program
GBR.............. Great Barrier Reef
GBRMPA ...... Great Barrier Reef Marine Park Authority
GLM.............. Generalised linear model
MMM............. Maximum monthly mean
NESP .... National Environmental Science Program
NOAA .... National Oceanographic and Atmospheric Administration
QLD .... Queensland
QPWS........... Queensland Parks and Wildlife Services
RHIS .... Reef Health Impact Survey
SST............... Sea Surface Temperature
TWQ.............. Tropical Water Quality

ABBREVIATIONS

C .... Celsius
eq.................. equation
et al............... and others
e.g................. for example
i.e.................. in other words
km................. kilometres
m................... metres
°S .... degrees south
%................... percent

ACKNOWLEDGEMENTS

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EXECUTIVE SUMMARY

Coral loss is of great concern on the Great Barrier Reef (GBR), with losses primarily attributed to tropical cyclones, predation due to Crown-of-Thorns Starfish (COTS), and coral bleaching. Historically, tropical cyclones were widely considered the leading driver of coral decline. However, within the context of climate change, global bleaching events have become more frequent. There is concern that bleaching on the GBR has increased its relative contribution to coral decline and mortality, particularly with the recent 2016 and 2017 bleaching events, and subsequent increases in global ocean temperatures. Understanding the relative contribution of bleaching to coral loss is an important step in developing appropriate strategies for protecting coral on the GBR. This report seeks to quantify the proportion of coral that was bleached and subsequently died as a result of bleaching using available data during the 2016 and 2017 bleaching seasons through data-driven modelling.

In order to accomplish this goal, we used an extension to the popular machine learning algorithm, random forests, called quantile regression forests. The quantile regression forests algorithm allows us to obtain prediction uncertainty as well as an estimate of coral bleaching and dead coral as a result of head stress. We model the proportion of coral that was subject to bleaching in various severity categories, as classified by the Reef Health Impact Survey (RHIS) protocol, and the proportion of coral mortality as a function of key heat stress metrics, namely degree heating weeks (DHW). DHW is a measure of intensity and duration of heat stress experienced in a marine environment. Multiple models were developed, including versions that allow for extrapolation across the entire GBR with available data.

Our models predict the proportion of coral bleached and the proportion of coral that died as result of marine heat stress (and hence bleaching) in 2016 and 2017, as well as providing a framework for prediction in future bleaching events (including 2019 and 2020). Our method also allows us to quantify prediction uncertainty in bleached coral and mortality. Our model predicts 42% (95% CI: 10% - 82%) of the coral on the GBR bleached to some degree in 2016, and in 2017 that 46% (95% CI: 12% - 82%) of corals bleached. We further predict that across the GBR 7% (95% CI: 1% - 22%) of coral died as a result of marine heat stress in 2016, while in 2017 6% (95% CI: 1% - 20%) died. Combined for 2016 and 2017, we estimate 9.3% (95% CI: 1% - 31%) of coral died. For 2019, our model predicts 18% (95% CI: 1% -50%) of coral bleached, and for 2020, we predict 53% (95% CI: 13% - 89%). Across the GBR, we estimate in 2019, 4% (95% CI: 0% - 24%) and in 2020, 8% (95% CI: 0% - 28%) of coral died due to marine heat stress.

1.0 INTRODUCTION

In 2012, De'ath et al. (2012) published a seminal paper outlining the degradation of coral on the Great Barrier Reef (GBR). Using a 27-year record of coral cover from representative reefs along the GBR they described a GBR-scale decline in coral cover of 50.7%. These losses were attributed to tropical cyclones (48% of loss), crown-of-thorns starfish (COTS, 42%), and coral bleaching (10%). Since that study, mass bleaching events have occurred across large parts of the GBR, notably the 2016 and 2017 bleaching seasons (Hughes et al., 2019a) and again in 2019 and 2020. These bleaching events were pan-tropical phenomena with studies indicating that 70% of global coral reefs were exposed to heat stress severe enough to cause coral bleaching (Heron et al., 2017, Hughes et al., 2018b). With climate change progressing at a rapid pace, coral bleaching is occurring more frequently (Hughes et al., 2018a). Given the increased occurrence of bleaching events, it's likely that the relative contribution of bleaching to coral mortality will have increased since De'ath et al. (2012) and will continue to accelerate further as the climate continues to warm. However, modelled projections for the health of the GBR depend strongly on parametrisations of bleaching mortality, which are currently based on limited empirical data and therefore have high levels of uncertainty (Condie et al, submitted). Coral loss also experiences spatial variation due to various factors such as environmental effects (Mellin et al., 2019a) and coral community composition (Mellin et al., 2019b).

Since bleaching events are occurring more frequently, it is critical to determine both the amount of bleaching that occurs during these events, and the amount of coral mortality that eventuates as a result bleaching from heat stress. This report seeks to build a model to quantify the amount of coral bleaching and mortality associated with bleaching due to marine heat stress on the GBR during the 2016 and 2017 bleaching events. The model analyses data from observations of coral bleaching and mortality, mapped to key climate change indicators of coral stress. We then use this model to predict the resulting coral bleaching and mortality in 2019 and 2020.

Coral reefs are sensitive to heat stress; even exposure to water temperatures 1°C above tolerance levels over 2-3 days can cause coral bleaching (Berkelmans and Oliver, 1999; Reaser et al., 2000). Corals live in a symbiotic relationship with microscopic algae (*Symbiodinium* spp.), in which the algae provide oxygen and nutrient rich food to the coral through photosynthesis in exchange for the coral structure's protective environment. Under heat stress, the algae's photosynthesis process breaks down, with the algae becoming toxic to the coral and being expelled (Hoegh-Guldberg, 1999). Because the algae provide coral with their colourisation, their loss typically 'bleaches' the coral white. They may recover from this state as more favourable conditions allow algae to recolonise the coral. However, more persistent and intensive warming can result in coral mortality as they are starved of nutrients and become more susceptible to damage from disease and other stressors (Wilkinson, 2008, Hughes et al., 2017; 2019).

The risk of coral bleaching is often expressed in terms of the accumulated heat stress. The product of the sea surface temperature anomaly above the maximum monthly mean (°C) and the duration of this warming (weeks) is referred to as degree heating weeks (DHW), usually calculated as a 12-week moving average. The link between DHW and coral bleaching is already well established (Liu et al., 2003; Strong et al., 2003; Eakin et al., 2010; Kayanne, 2017). Values above 4°C-weeks typically cause some bleaching, with bleaching mortality becoming widespread above 8°C-weeks (Liu et al. 2003). Hence, if mortality occurs at 8 DHW then it might be caused by either an extended period of moderate warming (e.g. 1°C above the maximum monthly mean for 8-weeks) or a shorter more intense event (e.g. 2°C above the maximum monthly mean for 4-weeks).

Several studies have successfully modelled the extent of bleaching as a function of DHW using generalised linear models (GLM) (e.g. Hughes et al. 2017; Kumagai et al. 2018) or a generalised linear mixed model (e.g. Harrison et al. 2019). However, these GLM approaches focussed only on the presence or absence of bleaching (Kumagai et al. 2018; Harrison et al. 2019) or >30% bleaching on a reef (Hughes et al. 2017), leaving coral mortality to be inferred from Liu et al.'s (2003) DHW categorization. An alternative solution adopted for the current study is to model observed coral mortality directly as a function of marine heat stress measured as DHW. Hughes et al. (2018b) used generalised additive models (GAM) on 63 reefs in the GBR as a means of modelling the nonlinear relationship between DHW and mortality.

Li et al. (2017) suggest that GLMs may not be as accurate in prediction as random forests (Brieman, 2001), particularly in marine contexts (e.g. Shan et al., 2006; Li et al., 2011; Li et al., 2012). Indeed, random forests have seen success in modelling coral bleaching presence as a function of DHW amongst other climate predictors (Kumagai et al., 2018). It therefore is reasonable to base the present analysis using a random forest approach. Typical random forests predict using the mean estimation of an ensemble of regression trees. Since we are further interested in obtaining uncertainty estimates as well as a prediction, we use an extension of the random forest approach, known as quantile regression forests (Meinshausen, 2006).

This report develops a method for predicting coral bleaching and coral mortality during severe heat stress events and applies it to the 2016 and 2017 bleaching events on the GBR. We develop predictive models relating observed coral bleaching and coral mortality to available heat stress metrics, specifically DHW, from the 2016 and 2017 bleaching seasons. We then use these relationships to extrapolate across the GBR and provide predictions for total bleaching and mortality during the 2016 and 2017 events. We also use the built models to predict bleaching and mortality in the 2019 – 2020 events.

2.0 METHODS

2.1 Reef Health Impact Surveys

We used data available from multiple monitoring programs on the Great Barrier Reef collected using the Reef Health and Impact Survey (RHIS) protocol (Beeden et al., 2014; Great Barrier Reef Marine Park Authority, 2014). These monitoring programs include the Great Barrier Reef Marine Park Authority's (GBRMPA) Eye on the Reef (EotR) surveys, the Queensland Parks and Wildlife Services (QPWS) - GBRMPA joint Field Management Program (FMP), and the Crown of Thorns Starfish (COTS) Control Program. Importantly, while the data was collated from multiple monitoring programs, data collection in these programs is standardized and follows the RHIS protocol with all observers trained to the same standard (Beeden et al., 2014; Westcott et al., 2020).

RHIS data was available from 8 January 2012 through 6 February 2020. From 2012 through 2016, RHIS data was primarily available between latitudes 16-17°S, expanding southward to 23°S from 2017 and northward to 12°S from 2019. For our purposes, we only utilise data over the period and area of highest water temperatures where nearly all the bleaching occurred (January through May over latitude bands of 16.078-16.948°S in 2016 and 16.113-16.938°S in 2017).

RHIS data is "point" based in which a 78.5m^2 circular area is extensively surveyed. A RHIS observation is conducted by first establishing a central point and associated perimeter of a circle with a 5m radius from that central point. Divers then survey the area carefully, recording estimates of coral conditions including coral cover and potential causes of impact on coral (Beeden et al., 2014). As a result, RHIS surveys are relatively precise, giving an accurate representation of the conditions at a sample site.

As part of the RHIS, information pertaining to coral bleaching is collected by determining the proportion of coral life-forms bleached at different levels of severity. Severity is categorized from 0 (none) through 4. Category 1 indicates bleaching only on the upper surface. Category 2 indicates pale/fluoro bleaching which is very light to yellow. Category 3 indicates coral that is bleached totally white. Category 4 indicates recently dead coral that is lightly covered in algae. The total proportion of coral bleached per category can then be calculated by taking the average proportion of each coral type with each category of bleaching, weighted by the proportion of that coral type at the RHIS site. The total bleached proportion over all categories can then be calculated by summing the proportions of coral bleached over the 4 severity categories.

At each RHIS site, an estimate of the proportion of coral cover that is recently dead is made. Figure 1 shows scatterplots of the total proportion of coral reported as bleaching across all severity categories in each month from the RHIS samples collected for the years 2016 and 2017. RHIS data also includes the water depth of survey sites. Figure 2 shows boxplots of non-zero observations (for visual purposes only as otherwise the boxplot would be dominated by zero counts) of bleaching severity grouped by areas <5 m and areas >5 m, where the cut-off of 5 m is for illustrative purposes only. Figure 3 shows the scatterplots of the proportion of recently dead coral and DHW as well for the years 2016 and 2017 across the bleaching season. Since we are also interested to see if bleaching and coral mortality are directly linked, we plot the recently dead coral proportion against the most severe bleaching categories, categories 3 and 4, for 2016 and 2017 in Figure 4.

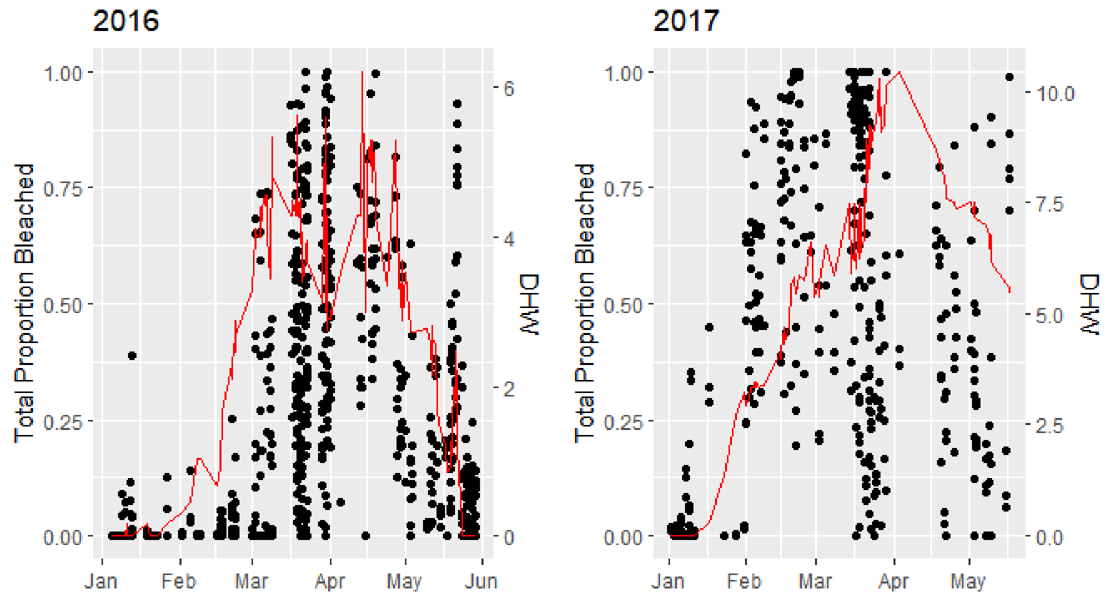

Figure 1: Plots showing total bleached proportion (black points) and DHWcurrent (red line) vs day for 2016 (left) and 2017 (right) bleaching season. The y-axis on the left side shows corresponds to bleaching proportion while the y-axis on the right side corresponds to DHW.

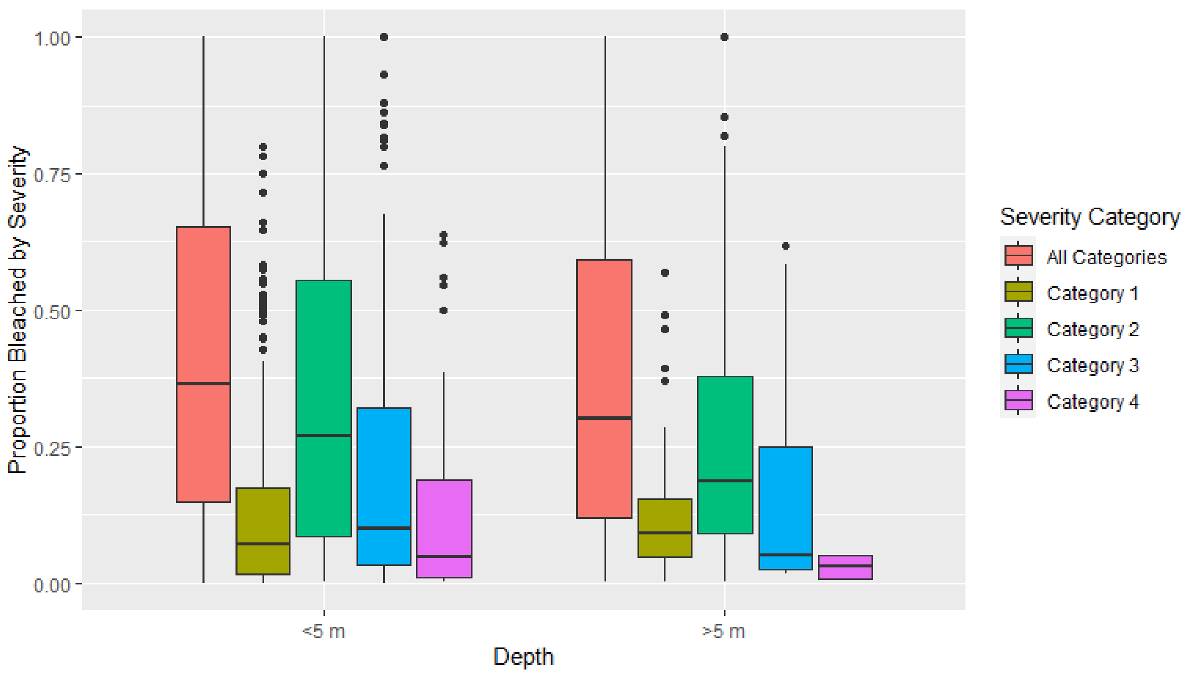

Figure 2: Boxplots showing the distribution of the proportion of bleaching in each severity category in years 2016 and 2017, grouped by depth above and below 5m. For clarity we only present non-zero bleaching proportions.

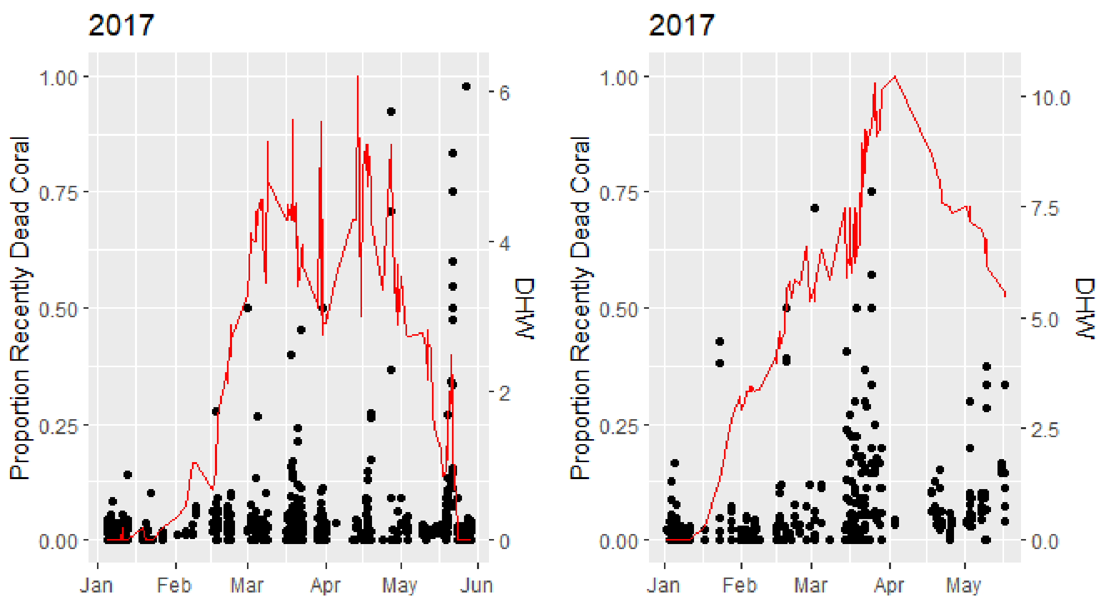

Figure 3: Plots showing proportion of recently dead coral (black points) and $DHW_{current}$ (red line) vs day for 2016 (left) and 2017 (right) bleaching season. The y-axis on the left side shows corresponds to bleaching proportion while the y-axis on the right side corresponds to DHW.

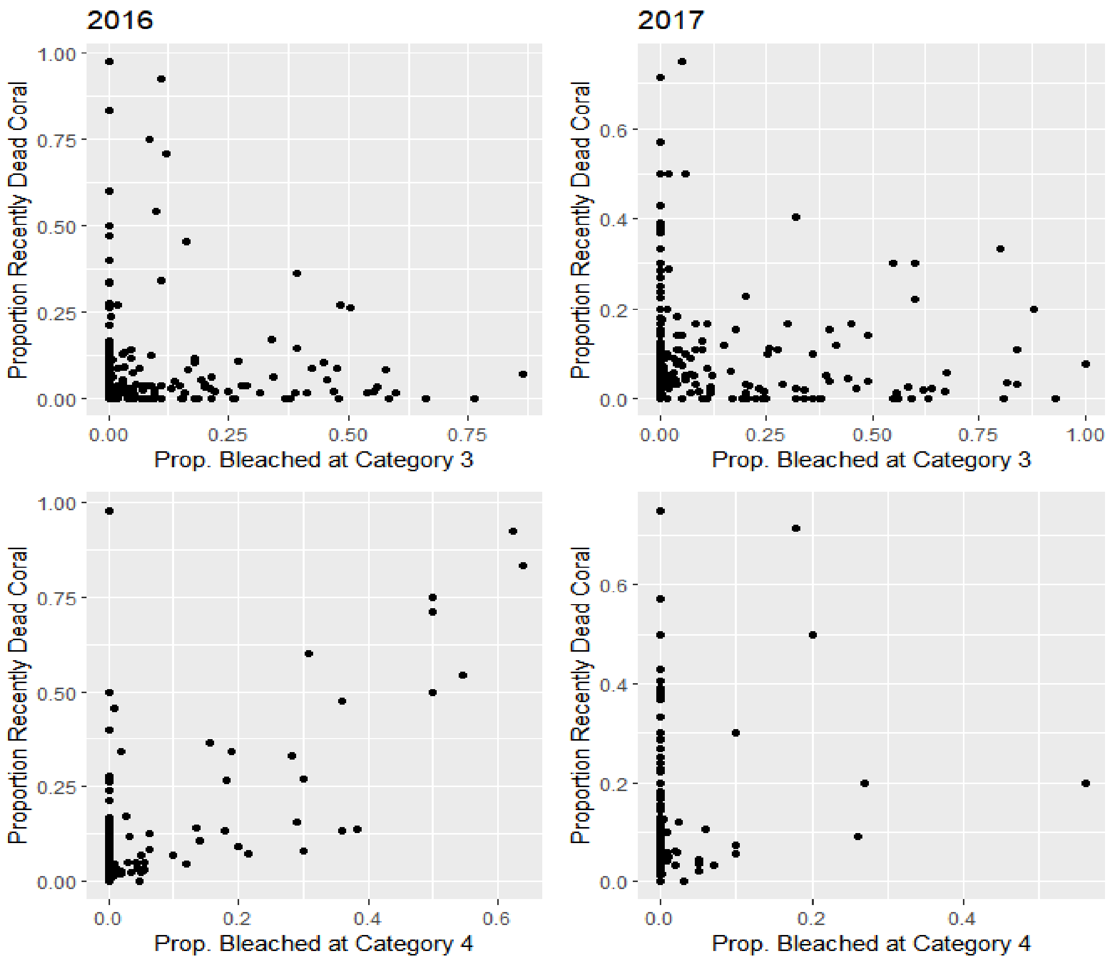

Figure 4: Plots showing proportion of recently dead coral (y-axis) vs proportion of bleached coral (x-axis) for 2016 (left) and 2017 (right) bleaching season. Top row shows bleached coral as category 3 and bottom at category 4.

2.2 Degree Heating Weeks

Coral bleaching potentially occurs with repeated heat stress over time, particularly at temperatures more than 1°C above normal conditions (Glynn and D'Croz, 1990). A key estimator of the degree of heat stress coral experiences is Degree Heating Weeks (DHW) (Liu et al., 2003). This measure is generally defined as an average of the difference between sea surface temperature and the typical summertime maximum. We utilize the specific definition from the National Oceanographic and Atmospheric Administration (NOAA) Coral Reef Watch (CRW) product. That is, for a given spatial location *i*, DHW is defined as:

$$DHW_i = \sum_{j=i-83}^{i} \frac{HS_j}{7}, HS_j \geq 1,$$

where HS_j is referred to as the HotSpot measure defined as the difference between sea surface temperature (SST) and the long-term maximum monthly mean (MMM). Because MMM is based on the long-term historical mean, it varies spatially but not temporally (Strong et al., 1997). Previous studies have stated that significant coral bleaching occurs at DHW of 4, and that mortality is likely at DHW above 8 (e.g. Liu et al., 2003, Strong et al., 2003; Eakin et al., 2010). Hence, a 2°C anomaly above MMM would be expected to cause significant bleaching after 2-weeks and significant mortality after 4-weeks.

We use the NOAA CRW product for DHW. This product contains daily values of DHW on a 5-kilometre (km) grid across the marine environments of the world. We restrict the pixels used from CRW to the GBRMPA boundary region. Figure 5 shows boxplots of DHW used for our analysis, grouped by years 2016 and 2017.

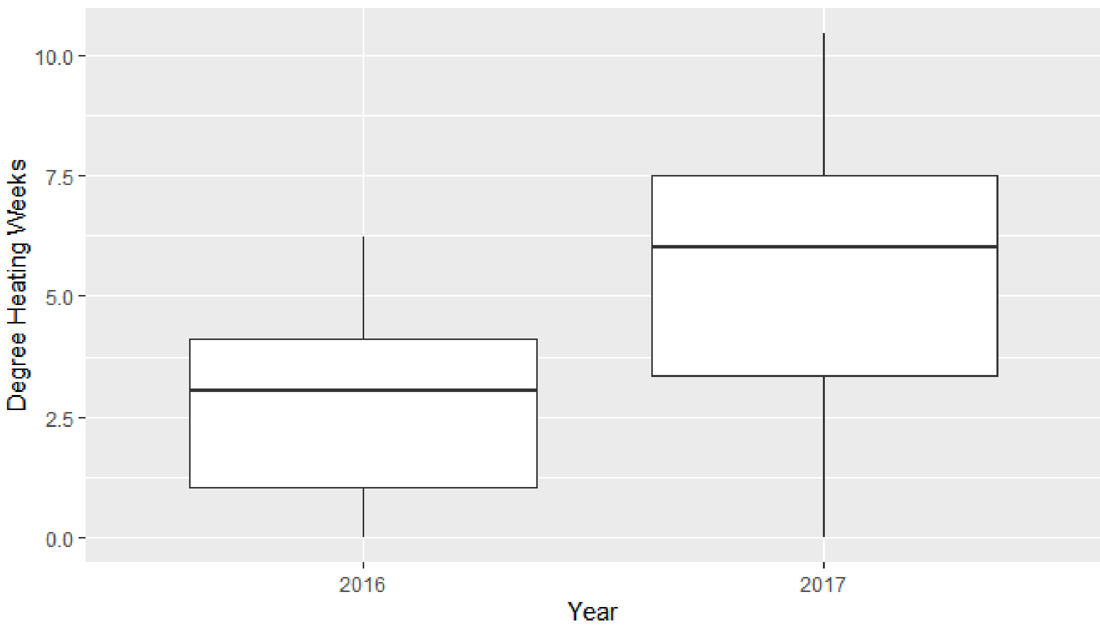

Figure 5: Boxplots showing the distribution of DHW divided by year.

2.3 Mapping DHW to the GBR

We match each RHIS observation to the closest 5 km pixel obtained from the CRW product by calculating the minimum Haversine distance (also known as great circle distance, accounting for the curvature of the earth) (Sinnott, 1984). DHW values are then calculated for each RHIS sample through the associated bleaching season. We then define two covariates associated with DHW: (1) the value of DHW on the day of the RHIS sample (hereafter referred to as $DHW_{current}$) and (2) the mean DHW value through the bleaching season for the year up to the day the RHIS sample was taken (hereafter referred to as DHW_{mean}). Figure 6 shows total proportion of bleached coral for 2016 and for 2017 against $DHW_{current}$. Figure 1 also shows the total proportion of bleached coral and $DHW_{current}$ against day for all RHIS samples in 2016 and 2017. Figure 7 shows the proportion of recently dead coral for 2016 and 2017 against $DHW_{current}$ as well.

Additionally, we used a dataset containing GBR features, including reef boundaries and type of features (e.g. reef or cay, amongst other labels) (Great Barrier Reef Marine Park Authority, 2007; Lawrey and Stewart, 2016). From this dataset, we extracted the centroid location and area (in km^2) of each coral reef. We mapped this feature data to the CRW product based on the centroid of each reef using the Haversine distance. For a given reef from this dataset, we calculate $DHW_{current}$ for 2016 and 2017 by determining the maximum value of DHW during the bleaching season and recording the day of that observation. We then calculate DHW_{mean} by taking the mean up to that day of the associated bleaching season.

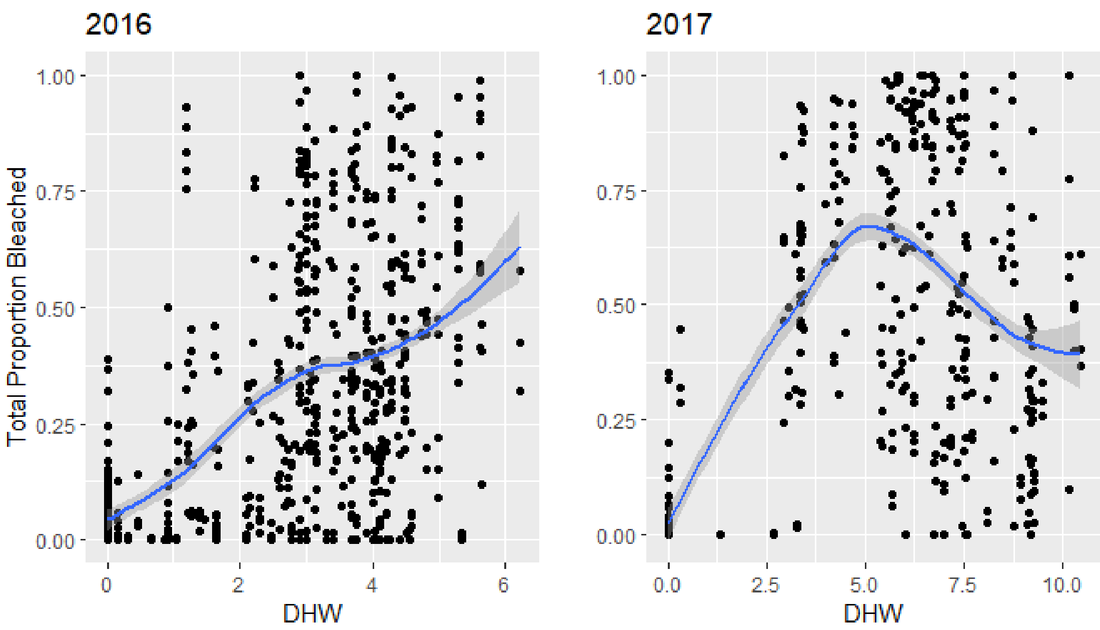

Figure 6: Scatterplots showing total proportion of bleached coral vs degree heating weeks for 2016 (left) and 2017 (right). A nonlinear fit is in blue.

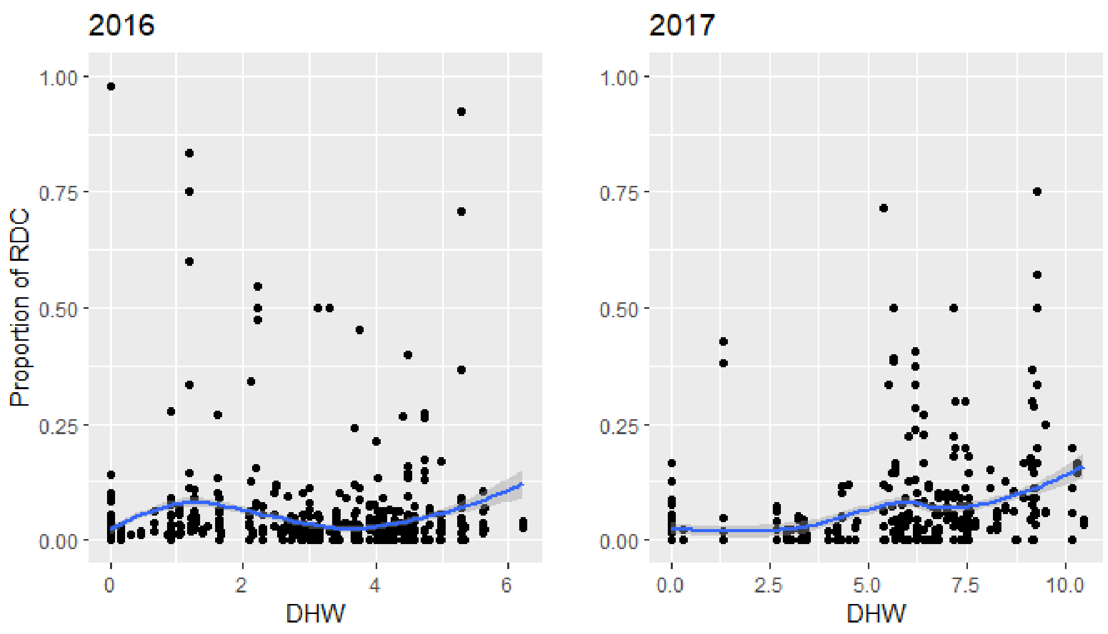

Figure 7: Scatterplots showing total proportion of recently dead coral vs degree heating weeks for 2016 (left) and 2017 (right). A nonlinear fit is in blue.

2.4 Analysis

We focus our analysis on modelling the proportion of bleached coral and the proportion of recently dead coral. Some explanatory variables, like depth, are not available at all locations in the GBR for prediction but are at observed locations. For that reason, we consider multiple sets of explanatory variables to explore the predictive power of variables that are available across the GBR and highlight the best these models can do. For bleaching, we use the proportion of bleached coral in different severity categories (categories 1 through 4), the total proportion of bleached coral (all 4 categories combined), and the proportion of bleached coral in severity categories 3 and 4. We further consider 4 different sets of explanatory variables:

- M1: $DHW_{current}$;
- M2: $DHW_{current}$ and DHW_{mean};
- M3: $DHW_{current}$ and depth of the RHIS sample;
- M4: $DHW_{current}$, DHW_{mean}, and depth of the RHIS sample.

For modelling the proportion of recently dead coral, in addition to explanatory variable sets M1-M4 above, we consider the following additional sets:

- M5: proportion at categories 1, 2, 3, and 4;
- M6: proportion at categories 1, 2, 3, and 4 and $DHW_{current}$;
- M7: proportion at categories 1, 2, 3, and 4 and $DHW_{current}$ and DHW_{mean};
- M8: proportion at categories 1, 2, 3, and 4 and $DHW_{current}$ and depth of the RHIS sample;
- M9: proportion at categories 1, 2, 3, and 4 and $DHW_{current}$, DHW_{mean}, and depth of the RHIS sample.

That is, M5 considers solely the effects of bleaching on recently dead coral while M6-M9 are all extensions of M1-M4 accounting for DHW as well as bleaching severity, respectively.

We build the relationship between the above covariates and the six possible response variables of proportion of coral bleached using quantile regression forests (Meinshausen, 2006), which is an extension of random forests (Briemann, 2001). Random forests have seen success in modelling coral bleaching as a function of thermal measures such as DHW (e.g. Kumagai et al. 2018), and as such are the basis of the approach we utilise to build a relationship between the proportion of bleached coral at various severity categories and DHW. The random forest algorithm is a non-parametric "black box" approach which creates an ensemble algorithm that averages amongst a 'forest' of decision trees. Specifically, for a set of covariate variables $\boldsymbol{x}_i \equiv (x_{i1}, \dots, x_{ip})'$ and response variables y_i, for $i = 1, \dots, n$ where n is the number of observations (e.g. number of RHIS samples in our case). Then, based on a bootstrap random sample of observations $(y_i, \boldsymbol{x}_i)$, a regression tree f_b is created, where each possible split in the tree is determined by a random subset of explanatory variables (called random feature selection). A collection of *B* number of regression trees is created in such manner, and averaged to create the final estimate:

$$y = f(\boldsymbol{x}) = \frac{1}{B}\sum_{b=1}^{B} f_b(\boldsymbol{x}).$$

For our purposes, we set *B* = 500 trees.

Quantile regression forests extends random forests by generating prediction intervals based on quantiles of the conditional distribution of the response variable given predictor variables. This is done by quantifying all observations for each split in a node of a tree as opposed to only the mean of the observations (as done in traditional random forests). This allows for estimation of prediction intervals using quantiles based on samples not used for estimation of each individual node. This is a critical extension that the standard random forest algorithm does not implement. For complete details of quantile regression forests, we refer the reader to Meinshausen (2006).

Models are fit in the statistical computing language R (R Core Team, 2020) using the "quantregForest" package (Meinshausen, 2017). This package utilizes the "randomForests" (Liaw and Wiener 2002) package as a base for building the forest. For model validation, we hold out 10% of the data as a test set and calculate the associated prediction intervals on this test set. We then determine the percent of observations in the test set that lie within the associated prediction interval.

We use the estimated quantile regression forest models to predict the amount of bleaching and predicted proportion of dead coral due to heat stress across the GBR for the 2016 and 2017 bleaching events. This is done by first assigning a DHW from the NOAA dataset for each reef, and then calculating a weighted mean across all reefs, using the area of each reef as weights. Due to lack of depth data across the entire GBR, we base these estimates of the proportion of total bleaching and bleaching by severity category on the best fit of M1 or M2. For the prediction of the proportion of dead coral due to heat stress, we also use the best model fit of M1 or M2. This is because severity bleaching categories, like depth, are not observed across the entire GBR and thus would need to be estimated. These estimates would have their own associated uncertainty, which would be propagated to the estimate of recently dead coral.

3.0 RESULTS

The quantile regression forest models were fit to bleaching data from 3228 available RHIS samples taken from 1 January through 31 May for the years 2016 and 2017. We apply the quantile regression forest modelling method described in Section 2.4 to this bleaching data.

3.1 Model Estimation

Table 1 shows the variance explained by each model for each response variable for the models M1 through M4. In general, M4 models, in which $DHW_{current}$, DHW_{mean} and depth were included explained the most variation, regardless of which bleaching category was modelled. This included the combined categories 3 and 4 and the total proportion bleached. M3 models explained less variation than the M4 models, followed by M2 and finally M1. Inclusion of depth in the model increased percent of variation explained more than did inclusion of DHW_{mean}, as evidenced by the increase from M1 to M3 compared to M1 to M2. This was the case in all response variables and severity categories of bleaching. The total proportion of bleached coral resulted in the models with the most explained variation, followed by category 2, category 3 and 4 combined, category 3, category 4, and finally category 1.

Table 1: Percent of variation explained by each random forest for models M1-M4 estimated. Percent of observations from the test set that lie within the 95% prediction interval for each random forest for models M1-M4 estimated.

RESPONSE	**M1** $DHW_{current}$	**M2** $DHW_{current}$ & DHW_{mean}	**M3** $DHW_{current}$ & depth	**M4** $DHW_{current}$, DHW_{mean}, depth
Total Bleached	68.86%	72.42%	80.85%	86.42%
Category 1	26.39%	34.28%	55.44%	62.07%
Category 2	56.44%	61.67%	75.58%	82.74%
Category 3	45.47%	55.25%	73.71%	78.65%
Category 4	49.33%	53.02%	60.25%	68.44%
Category 3 and 4	47.8%	57.65%	73.29%	79.08%
Prop Dead Coral	39.87%	43.7%	55.74%	66.54%

Table 2 shows the variance explained for models M5 through M9, estimating proportion of recently dead coral using the proportion of coral bleached by severity category. Similar to the results of M1 through M4, the variance explained increased with the inclusion of depth, $DHW_{current}$ and DHW_{mean}. However, interestingly, M8 and M9 showed very little increase in variance explained compared to M7, indicating that including either DHW_{mean} or depth, combined with $DHW_{current}$, would significantly increase predictive performance.

Table 2: Percent of variation explained by each random forest estimated M5-M9 for recently dead coral.

MODEL	COVARIATES	VARIANCE EXPLAINED
M5	Categories 1-4	59.19%
M6	Categories 1-4, $DHW_{current}$	72.61%
M7	Categories 1-4, $DHW_{current}$ and DHW_{mean}	89.37%
M8	Categories 1-4, $DHW_{current}$, depth	90.71%
M9	Categories 1-4, $DHW_{current}$, DHW_{mean}, and depth	91.54%

We validate our models by fitting the Quantile Regression Forests to 90% randomly sampled observations of the data, holding 10% out as a test set for validation purposes. We then calculate a 95% prediction interval using the associated lower and upper bound quantiles from the Regression Forest, then determine the percent of observations in the test set that fall within the prediction interval. Table 3 shows the percent of test set observations that lie within the prediction interval for models M1 through M4 while

Table 4 shows the same for M5 through M9. In all cases, the prediction interval captures at least 95% of the test observations. This means that our model likely estimates higher uncertainty, meaning our reported prediction intervals will be wider than expected. Thus, our results will give a conservative estimate of uncertainty.

Table 3: Percent of observations from the test set that lie within the 95% prediction interval for each random forest for models M1-M4 estimated.

RESPONSE	M1 $DHW_{current}$	M2 $DHW_{current}$& DHW_{mean}	M3 $DHW_{current}$, & depth	M4 $DHW_{current}$, DHW_{mean}, depth
Total Bleached	97.21%	97.52%	100%	99.38%
Category 1	98.14%	98.76%	100%	100%
Category 2	95.67%	96.59%	99.07%	99.38%
Category 3	97.83%	98.76%	99.69%	100%
Category 4	97.21%	97.52%	98.45%	98.14%
Category 3 and 4	96.59%	97.83%	98.76%	98.14%
Prop Dead Coral	96.9%	99.07%	99.69%	99.38%

Table 4: Percent of observations from the test set that lie within the 95% prediction interval for random forest estimated M5-M9 for recently dead coral.

MODEL	% OBS IN PI
M5	98.45%
M6	99.55%
M7	99.55%
M8	99.76%
M9	99.66%

Given the fact that the M4 models, which include $DHW_{current}$, DHW_{mean}, and depth, resulted in the best fit amongst M1-M4 models, we performed an importance analysis for each explanatory variable. Figure 8 shows the importance plots for M4 models for all 6 response variables considered. This importance measure is known as the Gini impurity, a measure indicating increase in mean prediction error of each training datapoint (known as out-of-bag error) if that explanatory variable were not used for estimation (see Ishwaran (2015) for details). Higher importance values indicate higher predictive power of the covariate (e.g. feature). In all models, depth was the least important variable. $DHW_{current}$ was the most important for total proportion bleached, category 2, and category 3 and 4 combined. DHW_{mean} was the most important for category 1, category 3 (though virtually identical to $DHW_{current}$), and category 4.

Regarding the models of the proportion of recently dead coral, we present the results of M5 (in which only proportion of bleaching by category are used as covariates), M7 (inclusion of all covariates except depth) and M9 (inclusion of all covariates), given that M7 explained nearly the same amount of variation as M9. Figure 9 shows the importance plots for these models. Bleaching at category 4 was the most important variable in predicting recently dead coral across all three models, but DHW_{mean} was second in M7 and M9 models, followed by $DHW_{current}$. Interestingly, DHW_{mean} being more important than $DHW_{current}$ suggests that accumulated heat stress through the bleaching season is a better predictor than observed heat stress on the day, and perhaps should be investigated in future studies. Category 3 was the least important variable.

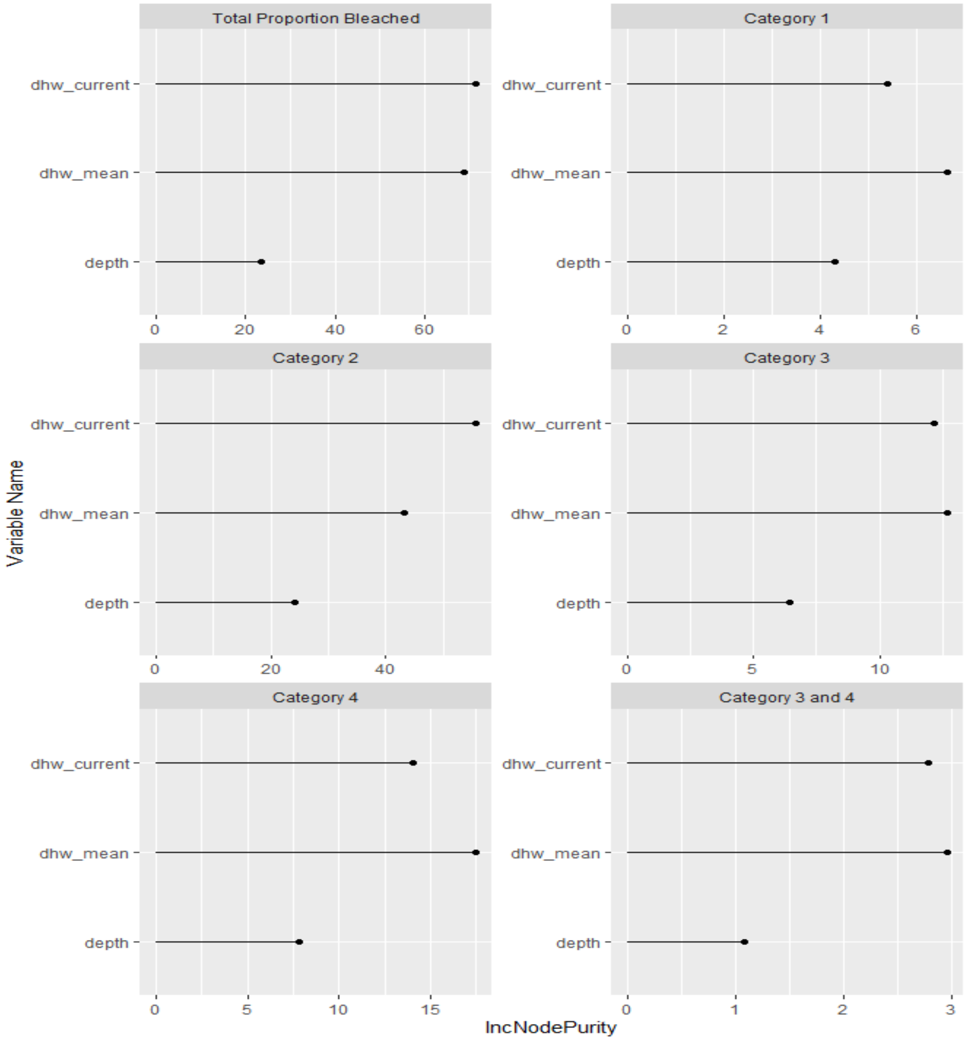

Figure 8: Importance plots of M4 models for each response variable.

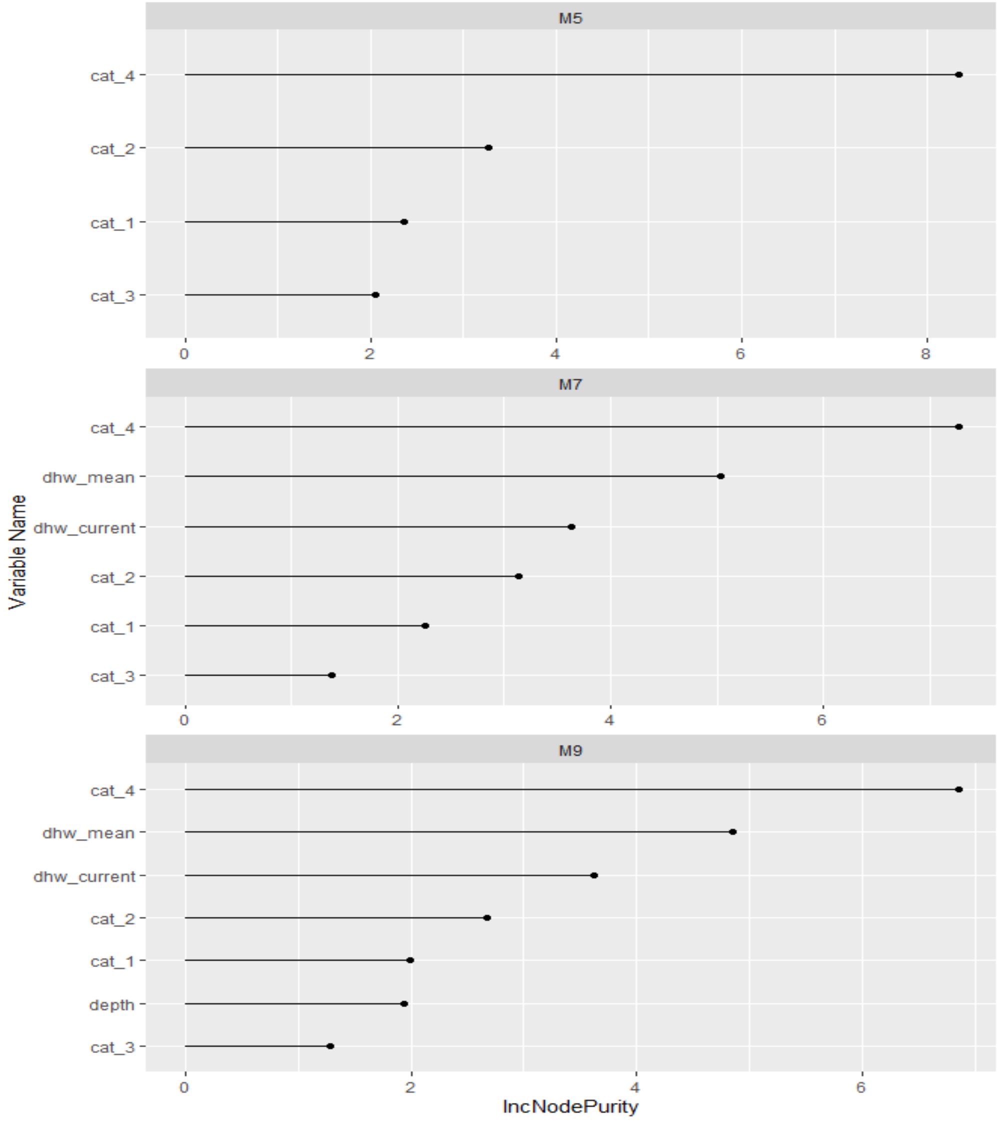

Figure 9: Importance plots of M5, M7, and M9 models for proportion of recently dead coral.

3.2 Estimation of 2016 and 2017 Bleaching Events

We use the estimated random forest models to predict the proportion of coral bleached in total and by each severity category across the GBR during the 2016 and 2017 bleaching events. We use the dataset on reef area presented in section 2.3, using the maximum DHW for each reef during the 2016 and 2017 bleaching seasons for our estimate. Table 5 shows the area and proportion of the GBR exposed to different levels of heat stress as measured by DHW, classified according to the intervals of Liu et al. (2003). According to their analysis, severe coral bleaching is likely to occur at DHW above 4 and potential mortality due to bleaching at DHW above 8.

Table 5: Total area of the GBR and proportion subject to categorized DHW for 2016 and 2017 bleaching seasons, where DHW is the maximum value obtained per reef.

	2016		2017	
DHW	**AREA (KM^2)**	**PROPORTION**	**AREA (KM^2)**	**PROPORTION**
<1	5001.162	0.176	1054.138	0.037
1-4	7309.784	0.257	9412.696	0.331
4-8	6695.289	0.235	11212.034	0.394
>8	9449.351	0.332	6776.719	0.238

The available data to predict bleaching at the scale of the GBR does not contain depth. Therefore, we use the best fitting quantile regression forest that does not include depth, which is M2. Table 6 shows the prediction of the proportion of bleached coral on the GBR as well as combined categories 3 and 4, and the total proportion of bleached coral for 2016. Table 7 shows the same for 2017. Critically, for 2016, the quantile regression forest model predicts 42.53% of the GBR was bleched with a 95% confidence interval of (9.98%, 81.60%). For 2017, the model predicts 46.32% was bleached with a 95% confidence interval of (11.98%, 81.57%). Table 6 and Table 7 also show the estimated recently dead coral from model M2 for 2016 and 2017, respectively. The estimated proportion of dead coral in 2016 as a result of DHW is 6.96% with a 95% prediction interval of (0.803%,22.00%). For 2017, the predicted proportion of dead coral was 6.23% with a 95% prediction interval of (0.630%,20.22%).

Table 6: Estimated mean and 95% lower and upper bound for each response variable in terms of area and proportion of GBR reefs bleached for 2016.

	AREA (KM^2)			PROPORTION		
RESPONSE	**MEAN**	**LOWER BOUND**	**UPPER BOUND**	**MEAN**	**LOWER BOUND**	**UPPER BOUND**
Total Bleached	12102.79	2838.61	23219.76	0.42532	0.09976	0.81600
Category 1	2060.76	0.58	9269.36	0.07242	0.00002	0.32575
Category 2	7668.25	31.27	20988.41	0.26948	0.00110	0.73759
Category 3	2363.07	0.00	9237.78	0.08304	0.00000	0.32464
Category 4	273.79	0.00	2301.57	0.00962	0.00000	0.08088
Category 3 and 4	2781.19	0.00	9626.11	0.09774	0.00000	0.33829
RD Coral	1980.47	228.58	6259.46	0.06960	0.00803	0.21997

Table 7: Estimated mean and 95% lower and upper bound for each response variable in terms of area and proportion of GBR reefs bleached for 2017.

	AREA (KM^2)			PROPORTION		
RESPONSE	**MEAN**	**LOWER BOUND**	**UPPER BOUND**	**MEAN**	**LOWER BOUND**	**UPPER BOUND**
Total Bleached	13181.18	3409.34	23211.96	0.46322	0.11981	0.81573
Category 1	2494.71	1.20	9304.46	0.08767	0.00004	0.32698
Category 2	7713.00	32.88	20172.35	0.27105	0.00116	0.70891
Category 3	3162.12	0.00	10308.54	0.11112	0.00000	0.36227
Category 4	302.52	0.00	2212.80	0.01063	0.00000	0.07776
Category 3 and 4	3333.42	0.00	10457.76	0.11714	0.00000	0.36751
RD Coral	1789.48	179.17	5753.99	0.06289	0.00630	0.20221

We also consider the combined impact of these back-to-back mass bleaching events the scale of the GBR. We do this by adding the results of 2016 with the additional proportion of affected coral in 2017. For example, if a reef was predicted to have 30% bleaching in 2016 and 40% in 2017, then that specific reef will have 40% aggregated bleaching. However, if a reef was predicted at 30% in 2016 and 20% in 2017, then on the aggregate that reef is said to have 30% over the 2-year period. The results of combining 2016 and 2017 for all reefs are found in Table 8. This shows 53.16% of the GBR's reef area bleached in either or both 2016 and 2017, with a 95% confidence interval of 16.72% - 89.80%, and 9.35% of the coral to have recently died as a result of heat stress, with a 95% confidence interval of 1.30% - 31.11%.

Table 8: Estimated mean and 95% lower and upper bound for each response variable in terms of area and proportion of GBR reefs bleached for 2016 and 2017.

	AREA (KM^2)			PROPORTION		
RESPONSE	**MEAN**	**LOWER BOUND**	**UPPER BOUND**	**MEAN**	**LOWER BOUND**	**UPPER BOUND**
Total Bleached	15127.40	4756.56	25552.40	0.53161	0.16716	0.89797
Category 1	3377.79	1.79	11859.60	0.11870	0.00006	0.41678
Category 2	9853.97	63.95	23832.25	0.34629	0.00225	0.83752
Category 3	4511.51	0.00	14400.19	0.15855	0.00000	0.50606
Category 4	510.49	0.00	3996.95	0.01794	0.00000	0.14046
Category 3 and 4	4944.47	0.00	14789.62	0.17376	0.00000	0.51974
RD Coral	2659.20	368.94	8852.05	0.09345	0.01297	0.31108

The mean prediction on a spatial map for total proportion of bleached coral of the GBR for 2016 and 2017 can be found in Figure 10 as well as the proportion of recently dead coral combined alongside DHW used for prediction. Notably, the majority of higher DHW are north of 15°S latitude for 2016, and 11°S and 17°S latitude for 2017, with some higher DHW values north of 11°S on the outer shelf. This is also where the primary area of bleaching was predicted as well. However, the recently dead coral was predicted more widely across the GBR. The uncertainty estimates, represented by the 2.5th and 97.5th percentiles for the lower and upper bound, for bleaching are found in Figure 11 and for recently dead coral in Figure 12. Figure 13 and Figure 14 show the predicted proportion of bleaching in each severity categories 1-4 and categories 3 and 4 combined. There appears to be some correlation between the predicted reefs with higher proportions of category 4 bleaching (top row of Figure 14) and predicted values of proportion of recently dead coral (bottom row of Figure 10).

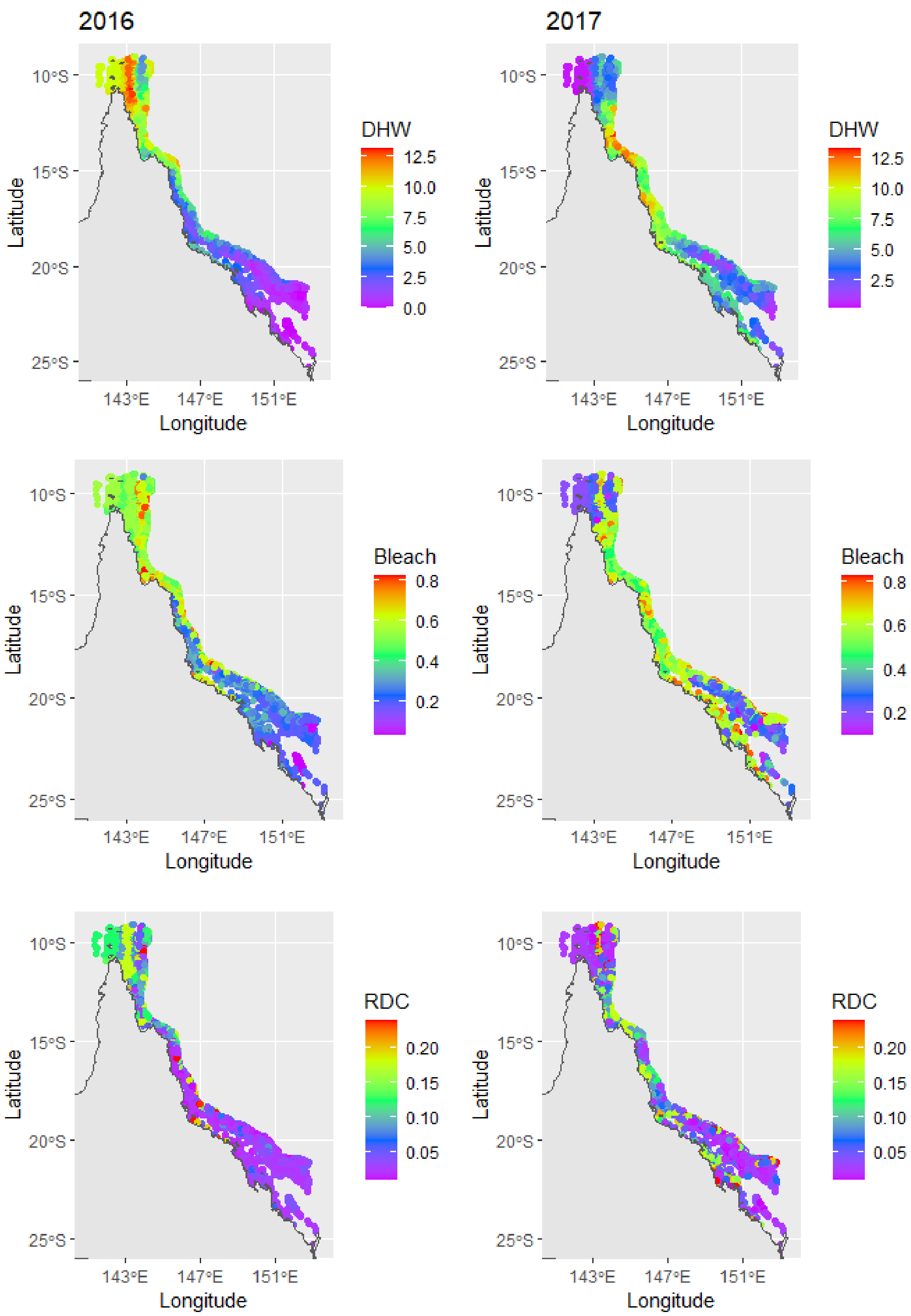

Figure 10: DHW (top) for 2016 (left) and 2017 (right), estimated total proportion bleached (middle) and estimated proportion of recently dead coral (bottom).

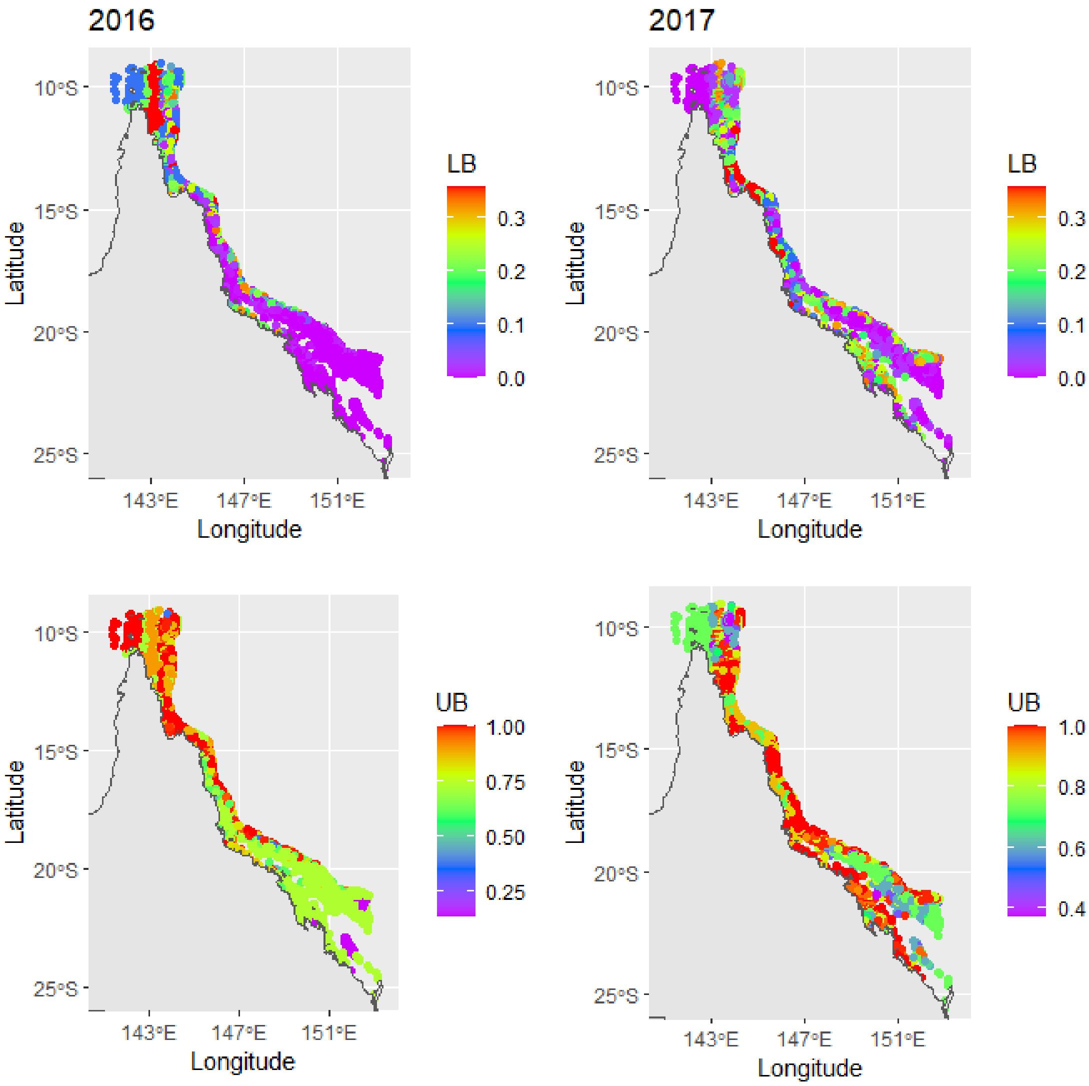

Figure 11: Lower (top row) and upper (bottom row) bleaching proportions for 2016 (left) and 2017 (right), representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds.

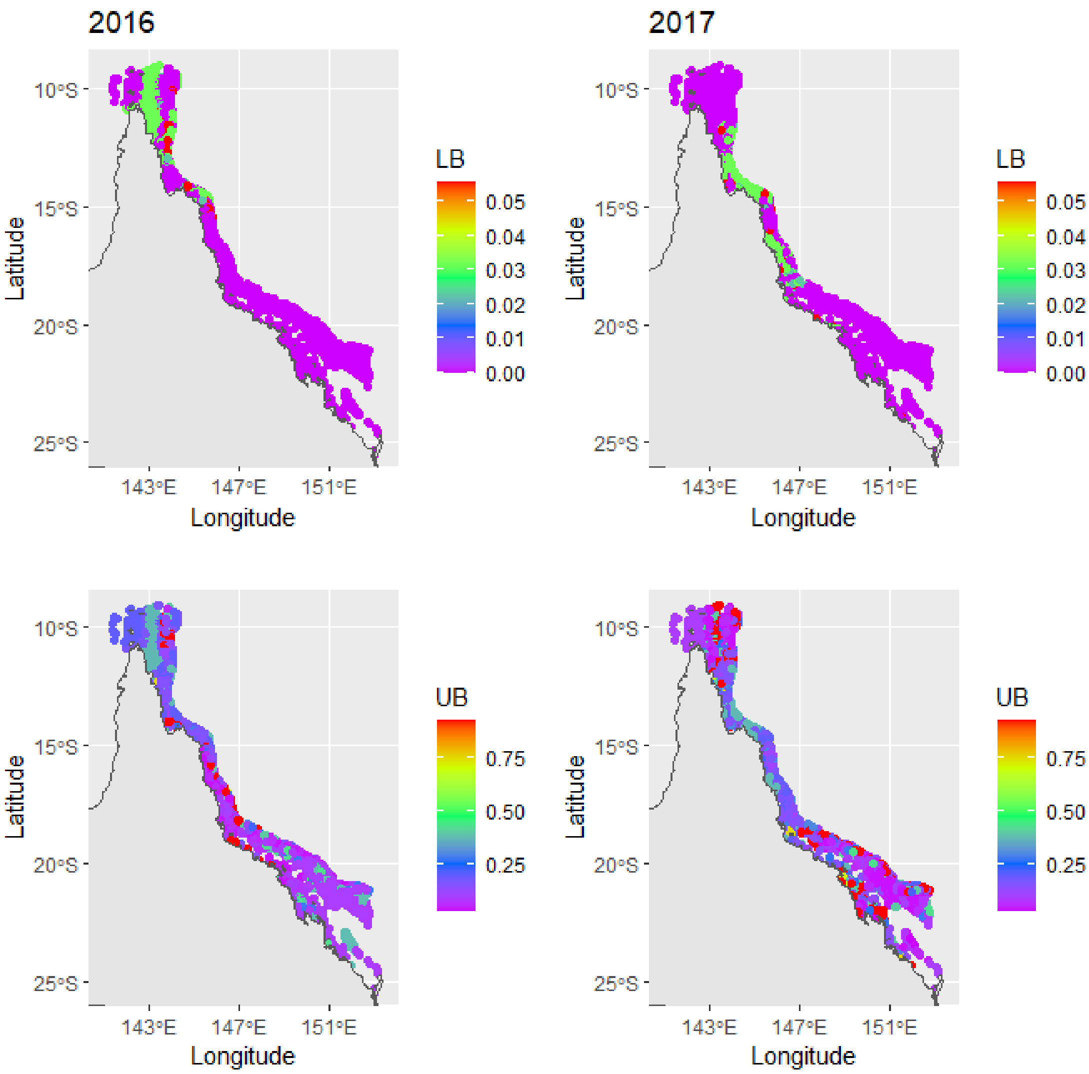

Figure 12: Lower (top row) and upper (bottom row) recently dead coral for 2016 (left) and 2017 (right), representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds.

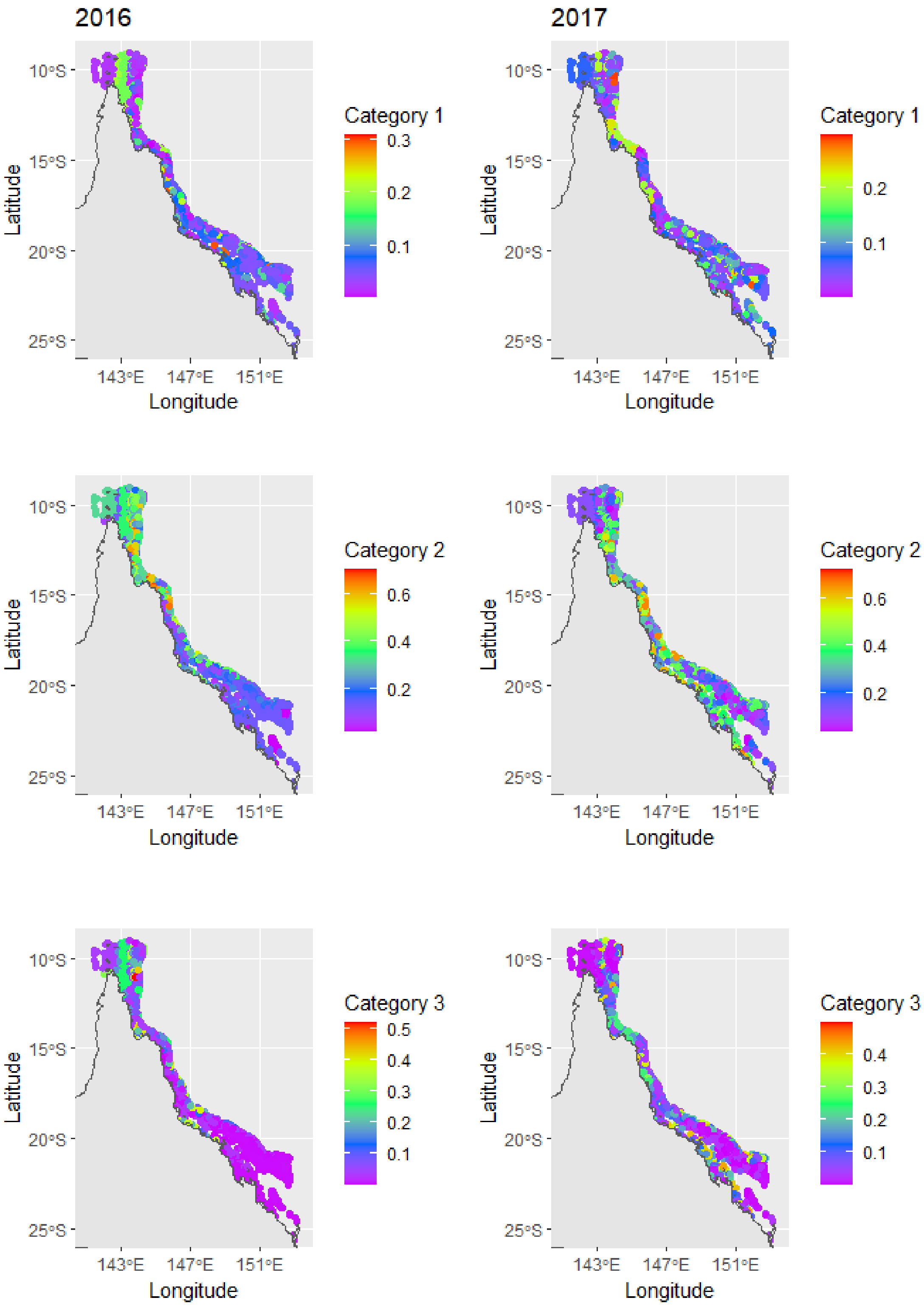

Figure 13: Bleaching proportions for 2016 (left) and 2017 (right) in category 1 (top row), category 2 (second row), and category 3 (third row).

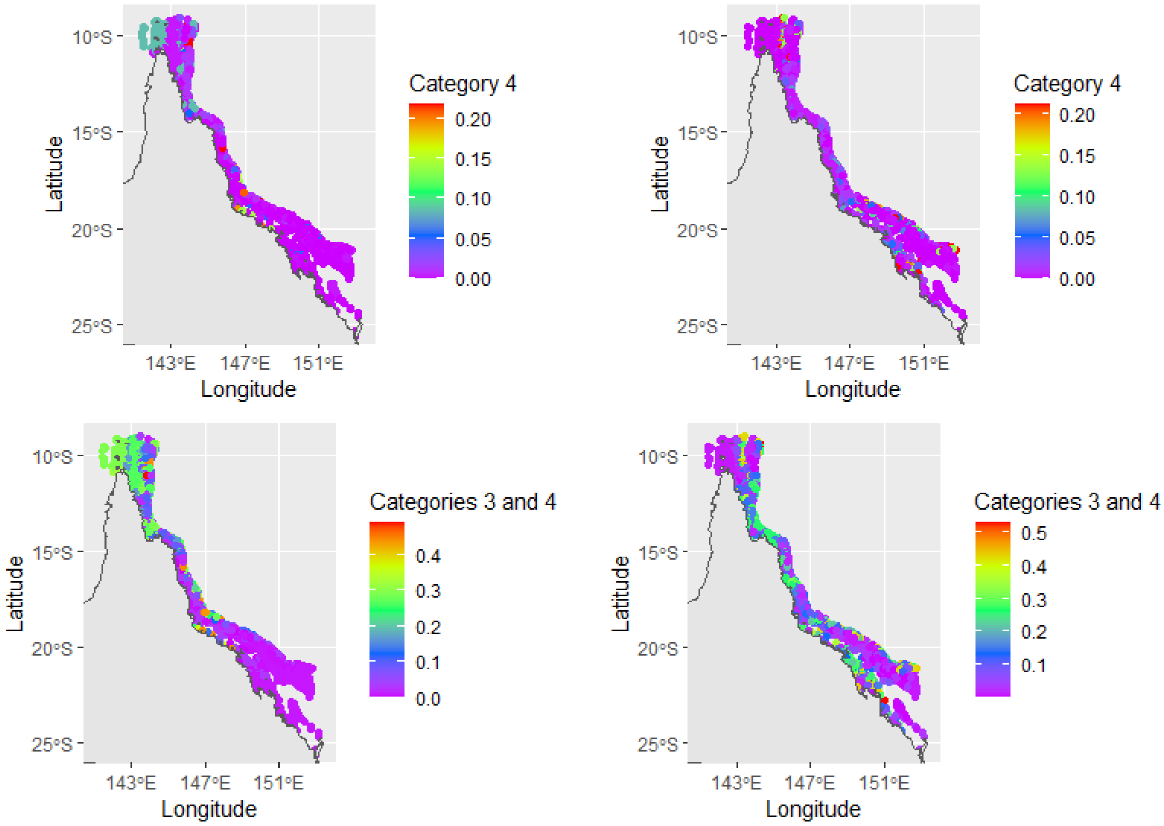

Figure 14: Bleaching proportions for 2016 (left) and 2017 (right) in category 4 (top row) and category 3 and 4 (second row).

Lastly, Figure 15 shows scatter plots of bleaching proportion against $DHW_{current}$ value, combining 2016 and 2017 together, and Figure 16 shows scatter plots of bleaching proportion against DHW_{mean} value for the two events combined. There is a noticeable increase in bleaching up to around DHW 5, when it appears to "level" in the amount of bleaching onward. These figures also show the proportion of recently dead coral against DHW. In particular, the proportion of dead coral peaks around 5 DHW. Figure 17 shows the estimated mean, lower bound, and upper bound of proportion of bleaching and recently dead coral when combining years 2016 and 2017.

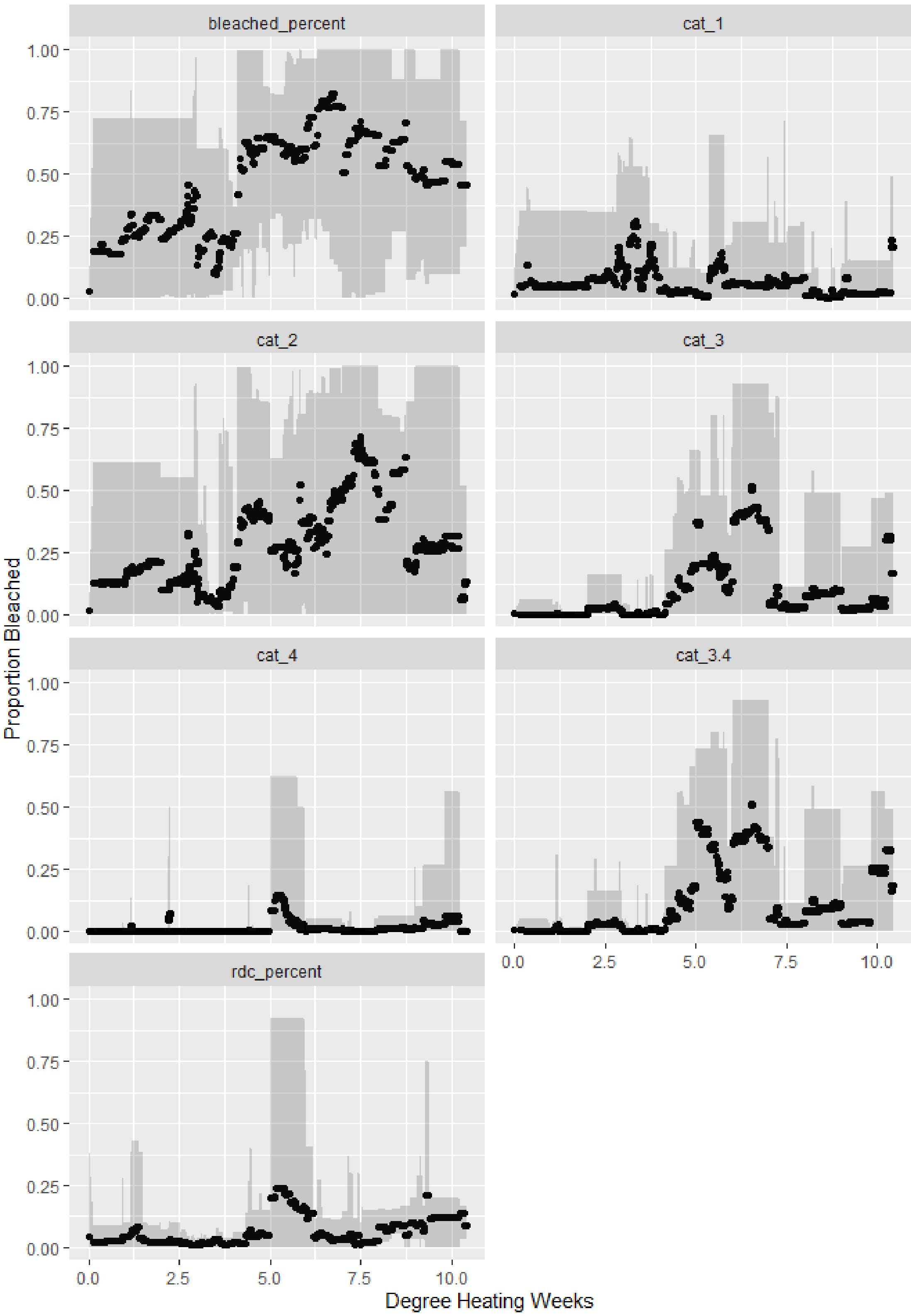

Figure 15: Proportion bleaching vs degree heating week observed.

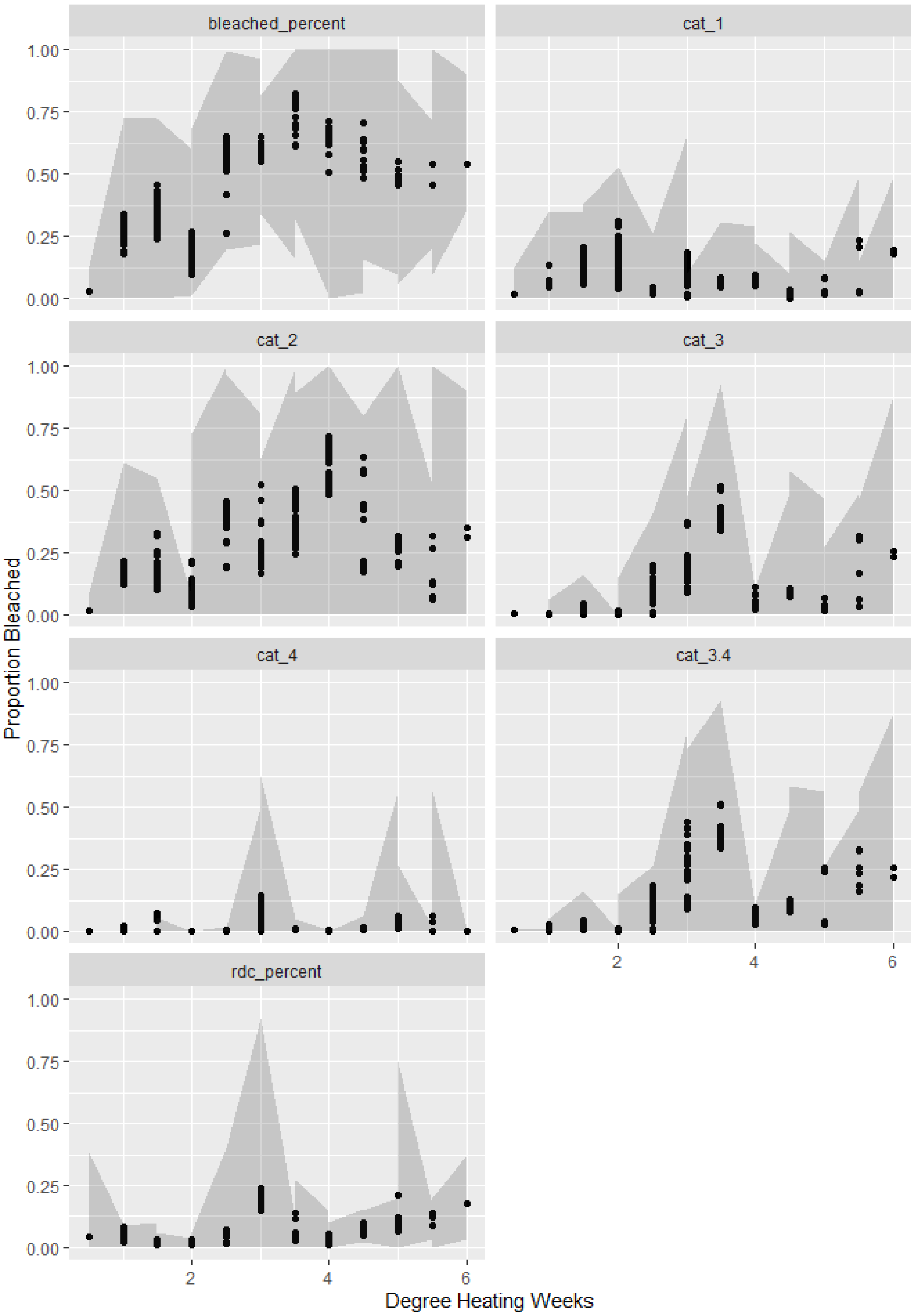

Figure 16: Proportion bleaching vs Degree heating week mean

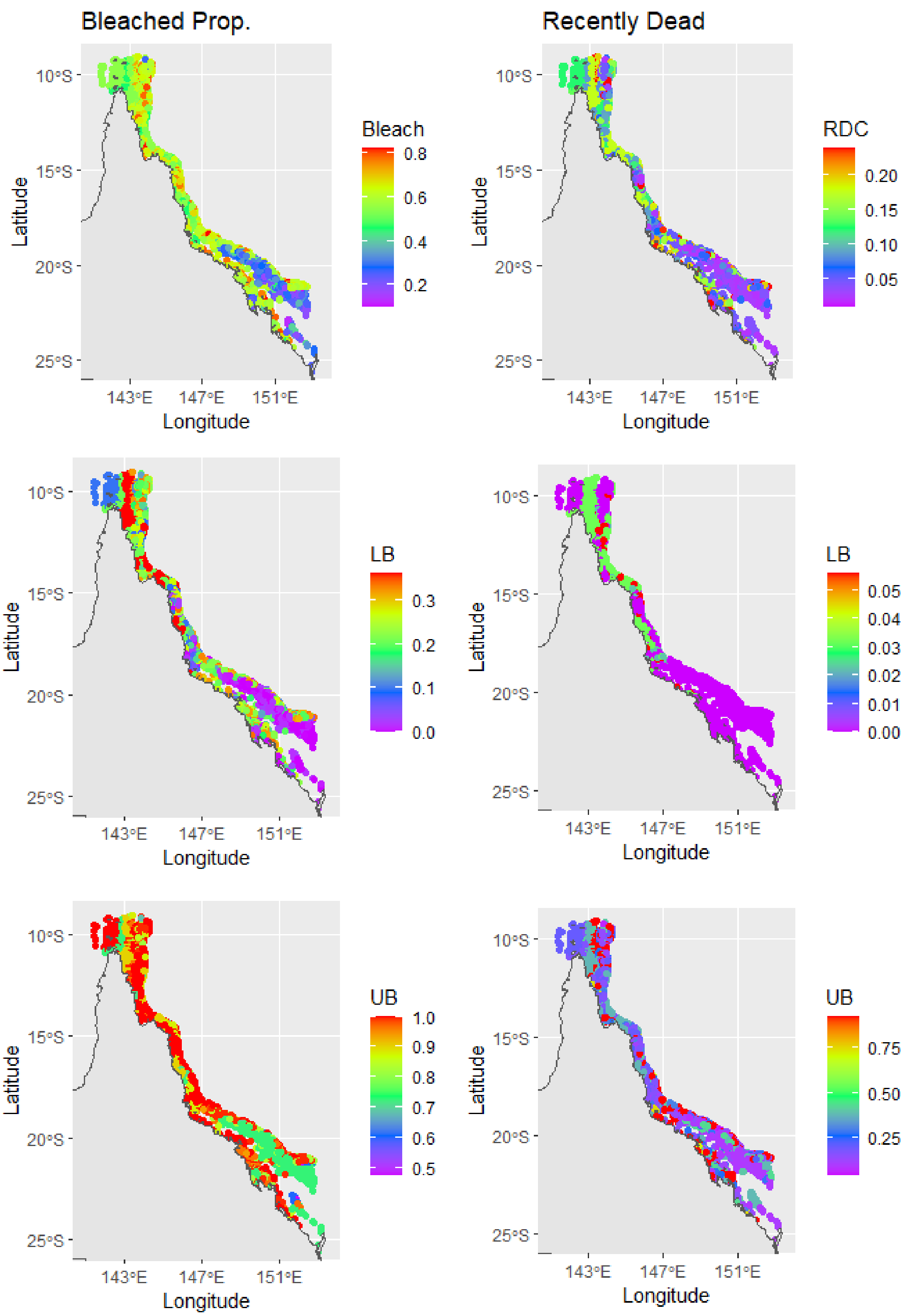

Figure 17: Estimated proportions of bleached coral(left) and recently dead coral (right) for combined years 2016 and 2017, representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds. Top row is mean estimate, middle is lower bound, and bottom is upper bound.

3.3 Estimation of 2019 and 2020 Bleaching Seasons

With concern focused on the potential for more frequent bleaching events in the future, in this section we present the random forest model predicts for the 2019 and 2020 bleaching seasons as an illustration of how this modelling framework might be used for assessing likely impacts of future events. We use the same methodology for prediction of 2016 and 2017 bleaching events in Section 3.2. We first map the associated maximum DHW value to each reef in the GBR. Table 9 shows the associated area and proportion of the GBR exposed to different groupings of DHW. Notably, 2020 saw nearly 79% of the GBR exposed to DHW greater than 4, with 23% exposed to DHW greater than 8.

Table 9: Total area of the GBR and proportion subject to categorized DHW for 2019 and 2020 bleaching seasons, where DHW is the maximum value obtained per reef.

	2019		2020	
DHW	**AREA (KM^2)**	**PROPORTION**	**AREA (KM^2)**	**PROPORTION**
<1	18631.010	0.655	230.7721	0.008
1-4	8019.369	0.282	5830.4265	0.205
4-8	1805.209	0.063	15839.3087	0.557
>8	0	0	6555.0798	0.230

Similar to extrapolating to the GBR scale for 2016 and 2017, we use the estimated M2 model, which uses $DHW_{current}$ and DHW_{mean}, to predict the total proportion of coral on the GBR that bleached as well as bleaching in each category, and recently died for 2019 and 2020 due to heat stress.

Table 10 shows the results for 2019 while Table 11 shows the results for 2020. For 2019, the model predicts that 18.03% of the GBR was bleached with 95% confidence interval of (1.32%, 49.87%). For 2020, the predicted bleaching increases to 52.78% of the GBR with 95% confidence interval of (12.78%, 88.55%), a higher value than predicted for 2017. The proportion of recently dead coral predicted from heat stress was 3.79% (0, 24.04%) for 2019 and 7.89% (0.46%, 28.23%) for 2020.

Table 10: Estimated mean and 95% lower and upper bound for each response variable in terms of area and proportion of GBR reefs bleached for 2019.

	AREA (KM^2)			PROPORTION		
RESPONSE	**MEAN**	**LOWER BOUND**	**UPPER BOUND**	**MEAN**	**LOWER BOUND**	**UPPER BOUND**
Total Bleached	5130.89	374.06	14191.44	0.18031	0.01315	0.49872
Category 1	1211.36	0.00	7322.27	0.04257	0.00000	0.25732
Category 2	3137.70	31.59	11744.44	0.11027	0.00111	0.41273
Category 3	450.74	0.00	1915.20	0.01584	0.00000	0.06730
Category 4	107.58	0.00	516.55	0.00378	0.00000	0.01815
Category 3 and 4	480.24	0.00	1974.49	0.01688	0.00000	0.06939
RD Coral	1078.04	0.00	6841.68	0.03788	0.00000	0.24043

Table 11: Estimated mean and 95% lower and upper bound for each response variable in terms of area and proportion of GBR reefs bleached for 2020.

	AREA (KM^2)			PROPORTION		
RESPONSE	**MEAN**	**LOWER BOUND**	**UPPER BOUND**	**MEAN**	**LOWER BOUND**	**UPPER BOUND**
Total Bleached	15018.12	3635.82	25196.26	0.52777	0.12777	0.88546
Category 1	1983.21	1.11	8750.68	0.06969	0.00004	0.30752
Category 2	9143.54	67.03	22573.31	0.32133	0.00236	0.79328
Category 3	3538.12	0.00	12125.53	0.12434	0.00000	0.42612
Category 4	471.49	0.00	3722.16	0.01657	0.00000	0.13081
Category 3 and 4	4042.11	0.00	12421.27	0.14205	0.00000	0.43651
RD Coral	2245.26	129.80	8033.22	0.07890	0.00456	0.28231

The spatial prediction map for total proportion of bleached coral and recently dead coral can be found in Figure 18, with lower bounds in Figure 19 and upper bounds in Figure 20. Figure 18 also shows the current DHW values at each reef used to predict bleaching and coral mortality. The relatively higher values of DHW for 2019 (noting overall the year was considerably cooler than 2016, 2017, and 2020 regarding accumulated heat stress on the GBR) were north of 11°S. A noticeable difference for 2020 was that high values for 2020 appeared spread across the GBR as opposed to more northerly for 2017. As expected, the bleaching primarily was predicted to have occurred in areas with higher DHW values. Coral mortality was low for 2019 on the GBR scale. For 2020, on average coral mortality appears to have predicted lower proportions at each reef than 2017, but more reefs are predicted to have had coral die due to heat stress. This shows the reasoning for higher uncertainty bounds and higher estimated total coral mortality for 2020.

Lastly, Figure 21 and Figure 22 show the predicted proportion of coral that was bleached at each severity category.

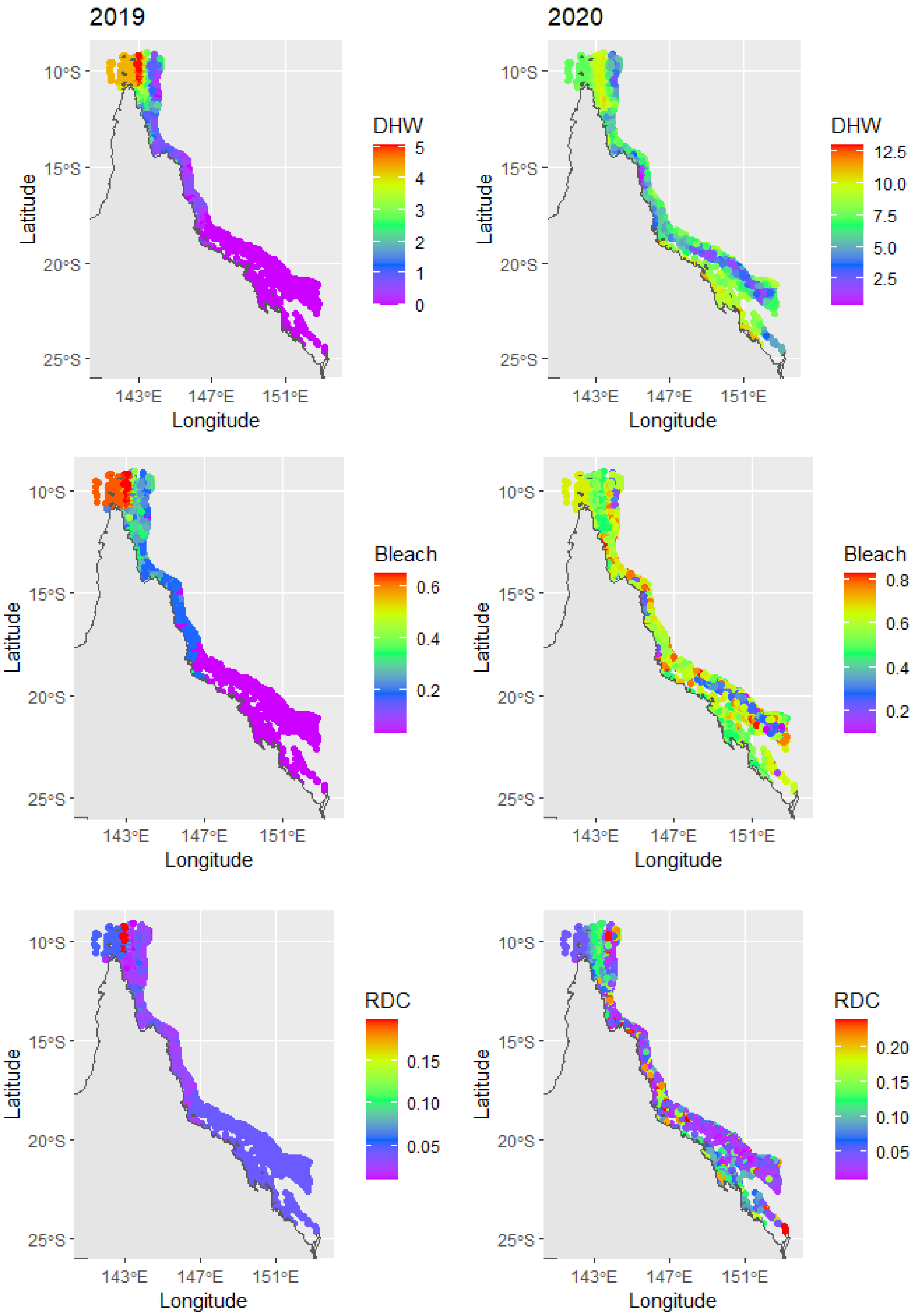

Figure 18: DHW (top) for 2019 (left) and 2020 (right), estimated total proportion bleached (middle) and estimated proportion of recently dead coral (bottom).

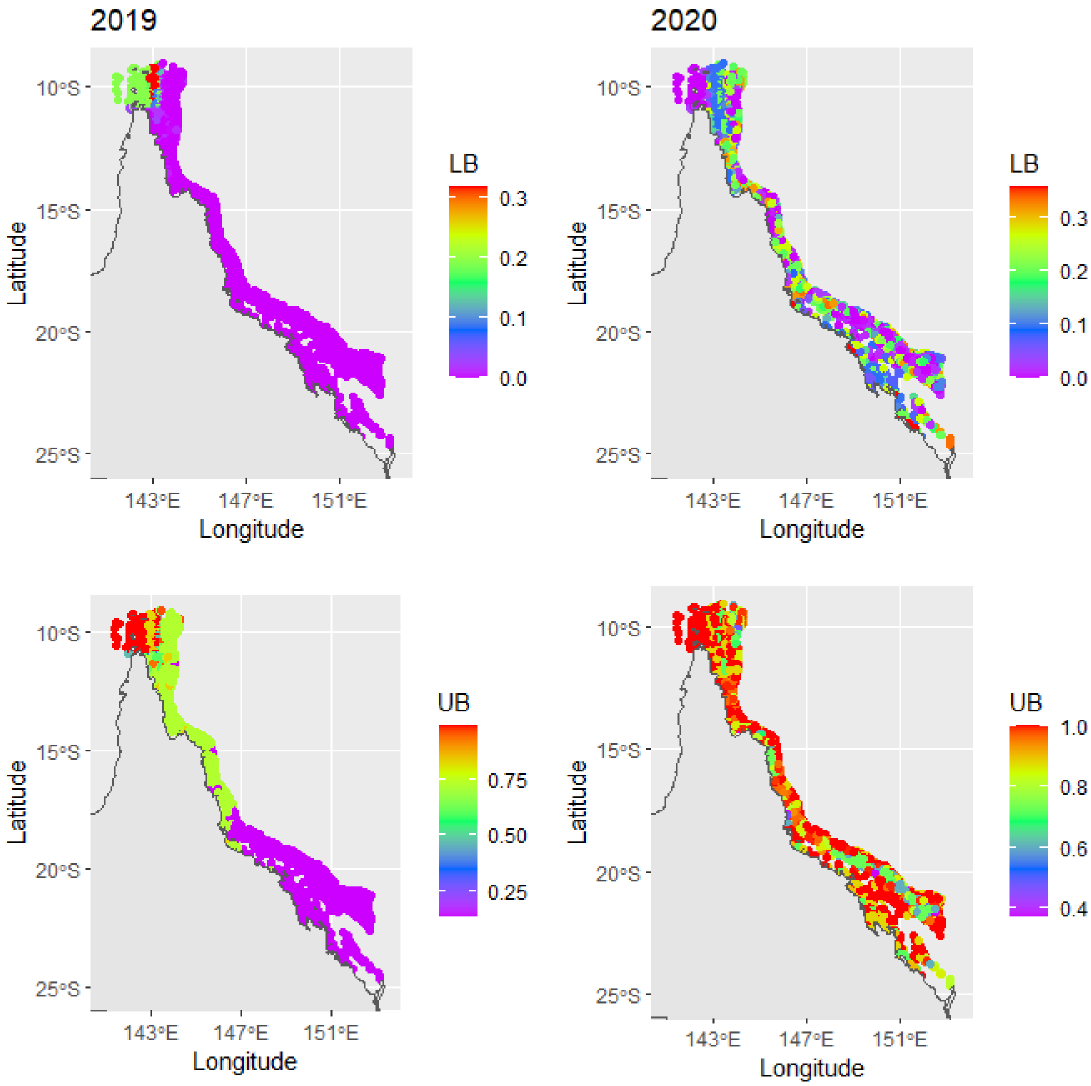

Figure 19: Lower (top row) and upper (bottom row) bleaching proportions for 2019 (left) and 2020 (right), representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds), representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds.

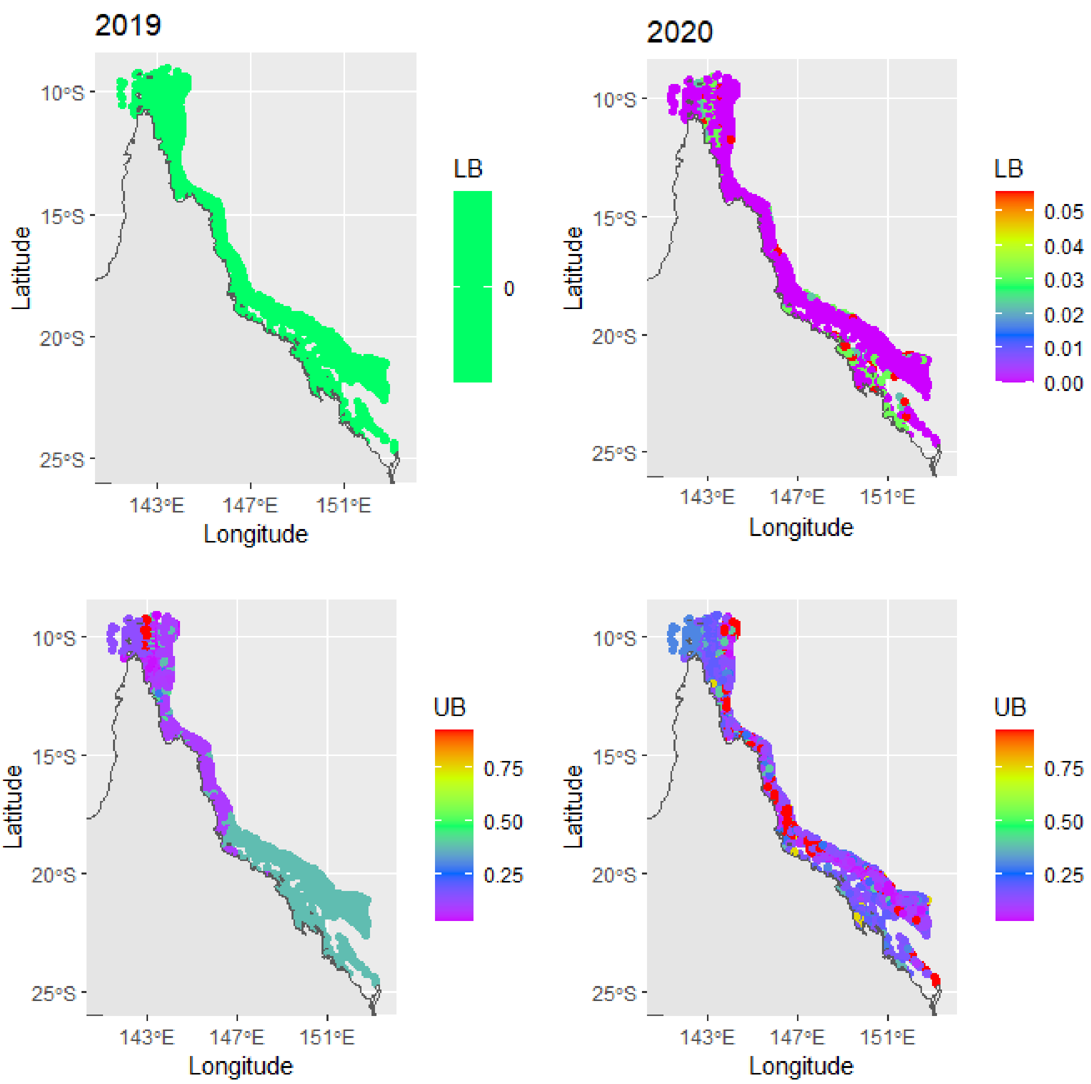

Figure 20: Lower (top row) and upper (bottom row) recently dead coral for 2019 (left) and 2020 (right), representing the 2.5th and 97.5th percentiles for lower (LB) and upper (UB) bounds.

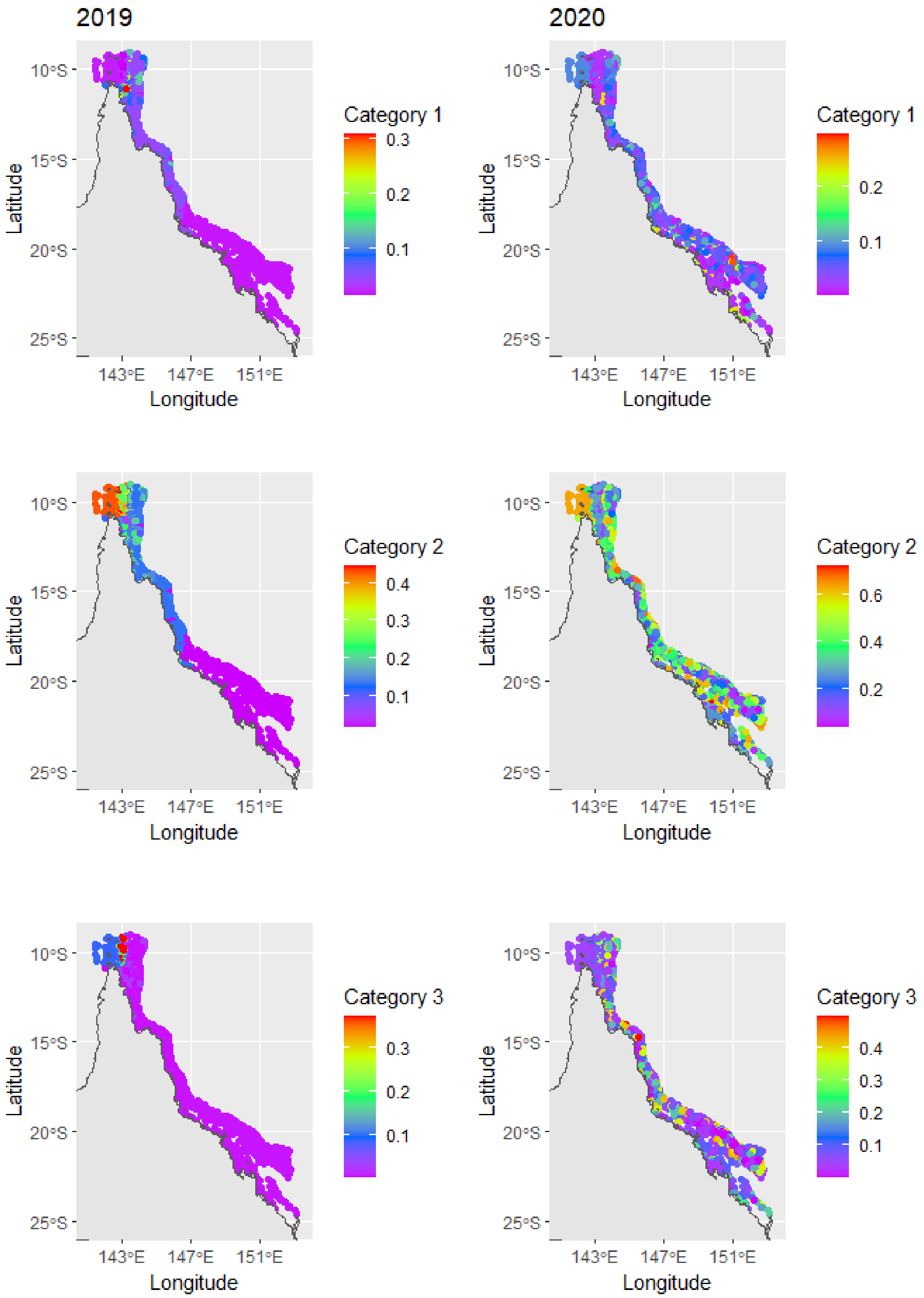

Figure 21: Bleaching proportions for 2019 (left) and 2020 (right) in category 1 (top row), category 2 (second row), and category 3 (third row).

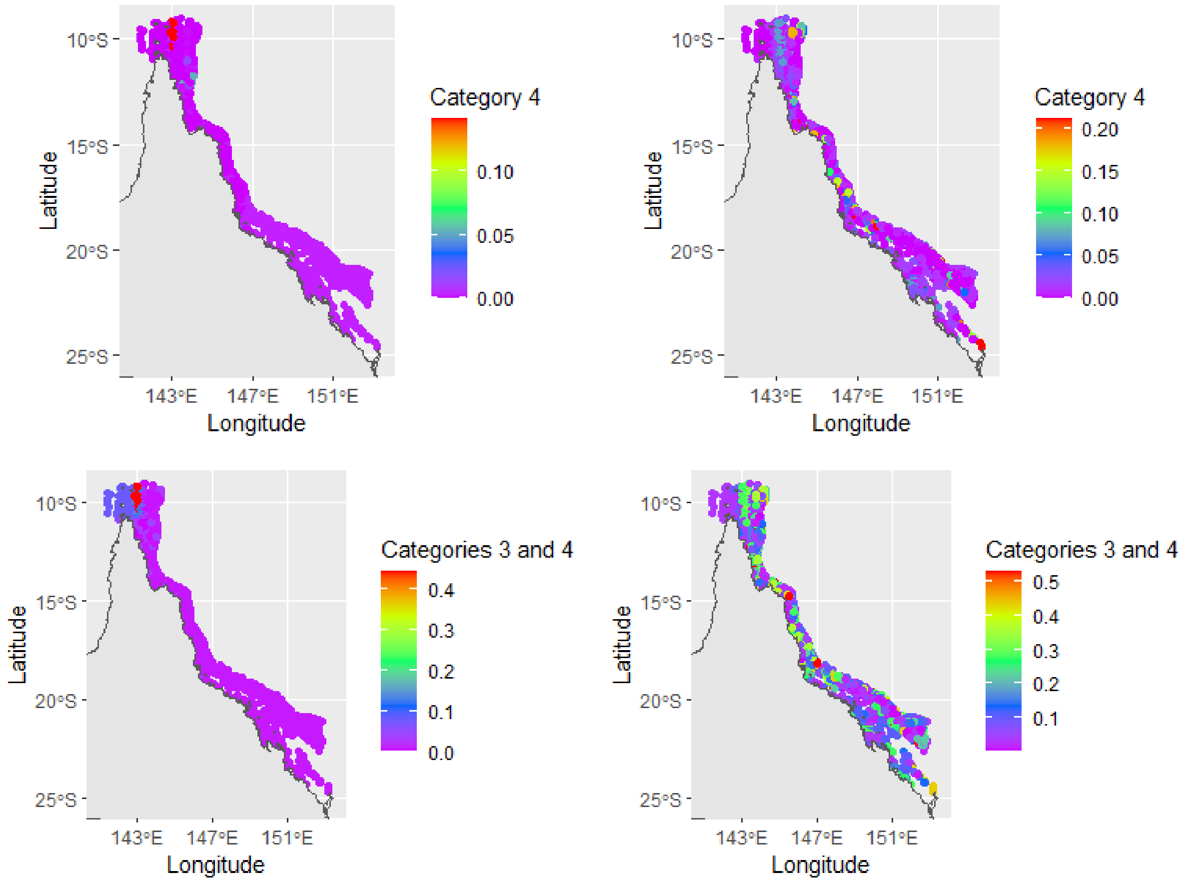

Figure 22: Bleaching proportions for 2019 (left) and 2020 (right) in category 4 (top row) and category 3 and 4 (second row).

4.0 DISCUSSION

Understanding how mass bleaching events translate into coral mortality at the scale of the GBR is far from straight-forward, but it is central to our ability to model its future trajectory and to formulate appropriate management responses. This task is complicated by the fact that field records of bleaching at a site represent snapshots of bleaching intensity but do not translate directly into coral mortality. Rather, the snapshot identifies a single point on a trajectory, the shape of which is influenced by site-specific hysteresis and subsequent conditions, and which only sometimes leads to coral mortality. In this analysis we have used predictions of the relationship between DHW and observed recently dead coral to predict the distribution of coral mortality on the GBR in the mass bleaching events of 2016 and 2017. We further used the models built using data from 2016 and 2017 to assess the likely impact of the bleaching conditions experienced in 2019 and 2020.

4.1 Comparison of Results with Previous Studies

The results of this analysis highlight the extent of bleaching and coral mortality due to heat stress. The predicted amount of the GBR bleached due to marine heat stress was 42% (95% CI: 10% - 82%) in 2016. For 2017, this was 46% (95% CI: 12% - 82%). Combining 2016 and 2017, an estimated 53% (95% CI: 18% - 90%) of coral on the GBR was bleached. The amount of coral that was predicted to have died as a result of marine heat stress in 2016 was 7% (95% CI: 1% - 22%). For 2017, this number was 6% (95% CI: 1% - 20%). Combining 2016 and 2017, the estimated coral mortality was 9.3% (95% CI:1% - 31%).

In their 2017 paper reporting on bleaching on mortality following the 2016 bleaching event, Hughes et al. report that upwards of 91% of reefs in the GBR experienced bleaching, with approximately 50% of reefs exhibiting severe bleaching, where >60% of colonies at the reef were bleached. These numbers cannot be directly compared to our analysis, which focused on the area of coral bleached rather than the proportion of reefs at which some coral experienced bleaching. However, if, on average, the 91% of reefs at which bleaching was detected in Hughes et al. (2017) experienced bleaching across roughly half their coral area, their results are similar to those reported here. Additionally, we look at the proportion of the GBR that was bleached in different severity categories, where category is defined by coral condition and not the proportion of bleaching on a reef, as Hughes et al. (2017) define. This provides additional information to the condition of bleaching for coral, and the likelihood that said coral will recover or die due to bleaching.

On the other hand, the coral mortality estimated in this study is lower than what is reported in Hughes et al. (2018b), where the long-term loss of coral cover across the GBR due to the 2016 bleaching event was estimated as 30%. However, that study explicitly identified two components to coral mortality following bleaching; “initial mortality”, relating to those corals killed immediately following the peak of bleaching in March 2016; and a longer term change in coral cover due to colonies that died over the following nine months, presumably as a result of increases stresses of bleaching. This study investigated data between January and May 2016, and so presumably underestimated the longer-term loss of stressed corals reported in Hughes et al. (2018b).

In addition, Hughes' et al. (2018b) estimates of coral mortality were based on bleaching severity scores from aerial surveys of 63 reefs, a much smaller and shallower (c. 2m) subset than were observed in-water to ground-truth bleaching and coral mortality, and the results from these were extrapolated across the GBR. Conversely, our analysis focussed on correlated fine-scale bleaching and mortality RHIS records, sampled across a subset of reefs on the GBR, then extrapolated to estimate GBR-wide outcomes. The two approaches thus capture different relationships explicitly and extrapolate different parts of the process to estimate bleaching and mortality across the GBR. The result is significantly different data sources and modelling approaches, which inevitably will result in different absolute estimates. However, our results agree with Hughes et al. (2018b) in that coral mortality starts at DHW values below 6. One advantage of the methods developed and presented here is the quantification of uncertainty in the estimate of coral mortality.

4.2 Data Driven Random Forest Modelling

We implemented an extension to random forests, namely quantile regression forests (Meinshausen, 2006), to predict the amount of coral that has bleached or died as a result of marine heat stress. In doing so, we were able to quantify prediction uncertainty of coral bleaching and mortality, as well as extrapolating across the GBR without making assumptions about the underlying distribution of the data. The downside of a random forest approach is the limitations of prediction of values within the range of the predictors (e.g. Hengl et al., 2018). In our analysis, the random forest was trained on observations with predictors up to DHW 10.5. That means, coral bleaching and mortality for DHW values above 10.5 were predicted to have the same value as 10.5. Without access to training data above 10.5 DHW, predictions for areas recorded above this level in our results are uncertain but probably conservative.

Random forests generally perform well "out of the box" and may have better predictive power than other GLM methods (e.g. Li et al., 2017). However, their predictions can be quite sensitive to the data that is used to train them (e.g. Hengl et al., 2018). With that in mind, the results presented in this analysis must be interpreted in terms of both the amount and quality of the training data. Though it is straightforward to predict across the GBR using the random forest models, there is still a need to have available covariates at appropriate spatial resolutions. For example, inclusion of covariates such as depth explained a higher percentage of the observed variation, but unfortunately was not available for all reefs. An important takeaway from this is that, in order to determine the coral mortality due to heat stress, more data is better, particularly with variables that may not change quickly through time (e.g. depth) or variables that can be collected via remote sensing (e.g. DHW).

4.3 Bleaching Severity as a Covariate for Mortality and Uncertainty

In modelling coral mortality as a result of heat stress, we investigated random forests models that used the different bleaching severity categories as covariates. Not surprisingly, this approach found that bleaching severity category 4 was the most important predictor of coral mortality. Importantly, however, we were also able to quantify how incorporating multiple bleaching severity covariates contributed to the prediction of mortality (e.g. 89.4% of the variance of recently dead coral explained by M7 compared to 43.7% for M2). The advantage in incorporating bleaching severity in a modelling framework results in a more accurate prediction of coral mortality. This is similar to the approach of Hughes et al in their 2018b paper, in which they interpolated bleaching severity at the reef scale. In that case, however, the uncertainty of the predictions produced was not rigorously defined. Our approach also highlighted the advantage of including seasonal average DHW alongside bleaching severity, as demonstrated by the increase in variance explained from M6 (e.g. 72.6% without DHW_{mean}) to M7 (e.g. 89.4%). This information should be used to inform parameterisation of a future model for marine heat stress related coral mortality.

One disadvantage of using bleaching severity to predict mortality in the current work, however, is the propagation of uncertainty. Using bleaching severity predictions using the current available data to predict coral mortality results in higher uncertainty bounds since the proportion of bleaching severity values are not observed across the GBR and need to be estimated. The uncertainty associated with the estimated proportion of bleaching severity in each category is propagated to the estimate of coral mortality. For reference, if we used the M7 model to predict coral mortality after predicting bleaching severity in categories 1-4 using the M2 models, the results are similar mean estimates but with wider confidence intervals. The estimate of coral mortality under this framework is 8.4% (95% CI: 2.0%, 42.8%) in 2016. For 2017, the estimate is 8.2% (95% CI: 1.9%, 35.4%). Projecting to 2019, the estimate would be 3.8% (95% CI: 0.0%, 24.0%), and for 2020, the estimate would be 7.9% (95% CI: 0.5%, 28.2%).

Although using bleaching categories as predictors resulted in higher uncertainty in this analysis, it also highlighted the fact that the proportion of bleaching at category 4 severity is critical. The similarity in results strengthens our confidence in the results of the M2 model. It also highlights another possible model in the next iteration, that being a Bayesian Hierarchical Model (Berliner, 1996), in which a complex model is split into simpler sub-models generally referred to as the data model, process model, and parameter model. In the context of predicting mortality as a result of bleaching, a mechanistic process model could be parameterised and then implemented with observed data mortality. Such models have seen success in data assimilation paradigms in climatology (Wikle and Berliner, 2007) amongst many other applications (see Cressie and Wikle, 2011). Even further, these models can also be used to improve parameterisation of bleaching in ecological models (Condie et al., Submitted). Such framework also allows one to quantify uncertainty in a rigorous manner and inform where our knowledge is lacking. For instance, a Bayesian Hierarchical Model will quantify the uncertainty of dead coral given the type of bleaching that occurs. This has the potential to provide invaluable information for preservation of the GBR in the presence of climate change. In addition, these models offer more flexibility than the random forest-based approach presented here, particularly in parameterisation (such as multinomial). In other words, there is plenty of scope to use cutting edge methods to improve prediction of coral mortality as a result of bleaching on the GBR.

4.4 Coral Variation, Resilience, and Future Analysis

In addition to the possible model extensions discussed above, this analysis suggests areas for future analysis. We aggregated bleaching data using observations from different coral life-forms. Different coral types are known to have different sensitivities and resilience to bleaching (e.g. Hughes et al, 2019b; Mellin et al., 2019b). There is also known spatial variation in coral community resilience amongst the inner, mid, and outer shelfs on the GBR in relation to bleaching (e.g. Mellin et al.,2019a). Indeed, the different sensitivities and resilience the various coral life forms have with respect to heat stress may explain the wide uncertainty bounds in the aggregate for total bleaching. The shift in coral bleaching and mortality around 5 DHW, as evidenced by Figure 15, may also indicate some coral functional groups are more resilient to heat stress, particularly when already exposed to heat inducing bleaching levels (e.g. Hughes et al., 2019b). This is supported in part by the noticeable non-linear nature of coral bleaching and mortality as a function of DHW, as evidenced by the data in Figures 6 and 7, as well as the results of the model, as evidenced by Figures 15 and 16. This suggests incorporating models that account for the different functional groups of bleaching is likely to be important in future analysis.

Lastly, this known spatial and community variation in resilience amongst coral life-forms with respect to bleaching and heat stress is likely to influence bleaching and marine heat stress related mortality estimates. While we incorporated seasonal/long-term estimates of DHW through DHW_{mean}, we recognise that this is not a perfect measure. Some coral lifeforms may not fully recover before successive bleaching events, and some that did survive may have resistance to future bleaching (Hughes et al., 2019b). Therefore, it stands to reason that estimates of the total proportion of coral that bleached or died as a result of marine heat stress without accounting for long-term effects may not be fully accurate. For example, coral may not have recovered form 2017 in time for the 2019 and 2020 bleaching seasons. This may also be the reason we see bleaching at DHW zero (e.g. Figure 6). Future analysis may incorporate longer term effects of coral degradation because of bleaching to build confidence in estimates for future events. However, we still contend that, because of the focus on proportion of bleaching as opposed to area, our results provide excellent starting estimates of the amount of coral that bleached and may have died as a result of marine heat stress.

5.0 SUMMARY

With global mass bleaching events during 2016, 2017, 2019 and 2020, coral mortality on the GBR due to marine heat stress has almost certainly increased from that first estimate in De'ath et al. (2012). Previous analyses, notably the work by Hughes et al. (2017; 2018a; 2018b), have quantified the amount of coral bleaching and mortality on the GBR at the reef scale with alarming estimates. This report builds on the ideas introduced in De'ath et al. (2012) and Hughes et al.'s various manuscripts to quantify bleaching and mortality as a result of marine heat stress with in-water measurements collected at a finer resolution; while estimating the uncertainty of predictions scaled up to the entire GBR. Importantly, this work used quantile regression forests, a non-linear machine learning approach, to estimate and quantify uncertainty of the proportion of coral that bleached and potentially died as a result of marine heat stress, as a function directly of key climate indicators, specifically DHW.

We estimate that a mean of 53% (95% CI: 18% - 90%) of coral on the GBR experienced bleaching during the 2016 and 2017 bleaching events, with overall morality estimated as a mean of 9.3% (95% CI: 1% - 31%). Using that same model, we estimated that 18% (95% CI: 1.3% - 49.9%) of the GBR bleached in 2019 and 52.8% (95% CI: 12.8% - 88.5%) in 2020. We estimated further that 3.8% (95% CI: 0.0% - 24.0%) and 7.9% (95% CI: 0.05% - 28.2%) of coral on the GBR in 2019 and 2020, respectively, died due to these marine heat stress events.

Critically, the work here provides a framework for determining the stress of coral at a finer resolution than previous studies, while also allowing those results to be scaled to the whole of the GBR. This is done via a data-driven approach, and easily allows for estimation of the amount of coral to die in the future because of marine heat stress. Further, this work can be used as a basis for predicting for future bleaching events to better inform reef managers. Such work could also be improved by incorporate long term effects of bleaching and coral mortality or incorporating coral functional groups into the analysis.

REFERENCES

Beeden R.J., Turner M.A., Dryden J., Merida F., Goudkamp K., Malone C., Marshall P.A., Birtles A. & Maynard J.A. (2014). Rapid survey protocol that provides dynamic information on reef condition to managers of the Great Barrier Reef. *Environmental Monitoring and Assessment*, 186, 8527-8540.

Berkelmans R. & Oliver J.K. (1999). Large-scale bleaching of corals on the Great Barrier Reef. Coral Reefs, 18:55-60.

Berliner, L. M. (1996). Hierarchical Bayesian time series models. In Maximum entropy and Bayesian methods (pp. 15-22). Springer, Dordrecht.

Breiman, L. (2001). Random forests. *Machine learning*, *45*(1), 5-32.

Condie S.A., Anthony K.R.N., Babcock R.S., Baird M.E., Beeden R., Fletcher C.S., Gorton R., Harrison D., Hobday A.J., Plagányi E.E., Westcott D.A. (submitted). Large-scale interventions may delay decline of the Great Barrier Reef. Royal Society Open Science.

Cressie, N., & Wikle, C. K. (2015). *Statistics for spatio-temporal data*. John Wiley & Sons.

De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27–year decline of coral cover on the Great Barrier Reef and its causes. Proceedings of the National Academy of Sciences, 109(44), 17995-17999.

Eakin CM, Morgan JA, Heron SF, Smith TB, Liu G, et al., 2010. Caribbean Corals in Crisis: Record Thermal Stress, Bleaching, and Mortality in 2005. PLoS ONE 5(11): e13969

Glynn, P.W., D'Croz, L. (1990). Experimental evidence for high temperature stress as the cause of El Niño coincident coral mortality. Coral Reefs 8, 181-191. https://doi.org/10.1007/BF00265009

Great Barrier Reef Marine Park Authority (2007). Great Barrier Reef (GBR) Features (Reef boundaries, QLD Mainland, Islands, Cays, Rocks and Dry Reefs) (GBRMPA), [Dataset]. Queensland, Australia: eAtlas Repository. https://eatlas.org.au/data/uuid/ac8e8e4f-fc0e-4a01-9c3d-f27e4a8fac3c

Great Barrier Reef Marine Park Authority (2014). Great Barrier Reef outlook report 2014. GBRMPA, Townsville, Qld, Australia.

Harrison, H. B., Álvarez-Noriega, M., Baird, A. H., Heron, S. F., MacDonald, C., & Hughes, T. P. (2019). Back-to-back coral bleaching events on isolated atolls in the Coral Sea. *Coral Reefs*, *38*(4), 713-7

Hengl, T., Nussbaum, M. Wright, M., Heuvelink, G., & Graeler, B. (2018). Random forest as a generic framework for predictive modeling of spatial and spatio-temporal variables. PeerJ. 6. e5518. 10.7717/peerj.5518.

Heron, S.F., Eakin, C.M., Douvere, F., Anderson, K.L., Day, J.C., Geiger, E., Hoegh-Guldberg, O., Van Hooidonk, R., Hughes, T., Marshall, P. and Obura, D.O., (2017). Impacts of climate change on World Heritage coral reefs: A first global scientific assessment.

Hoegh-Guldberg, O. (1999). Climate change, coral bleaching and the future of the world's coral reefs. Marine and freshwater research, 50(8), 839-866.

Hughes, T.P., Kerry, J.T., Álvarez-Noriega, M., Álvarez-Romero, J.G., Anderson, K.D., Baird, A.H., Babcock, R.C., Beger, M., Bellwood, D.R., Berkelmans, R. and Bridge, T.C., (2017). Global warming and recurrent mass bleaching of corals. *Nature*, *543*(7645), pp.373-377.

Hughes T.P., Anderson K.D., Connolly S.R., Heron S.F., Kerry J.T., Lough J.M., Baird A.H., Baum J.K., Berumen M.L., Bridge T.C., Claar D.C., Eakin C.M., Gilmour J.P., Graham N.A.J., Harrison H., Hobbs J.P.A., Hoey A.S., Hoogenboom M., Lowe R.J., McCulloch M.T., Pandolfi J.M., Pratchett M., Schoepf, V., Torda, G., & Wilson, S.K. (2018a). Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. Science, 359, 80-+.

Hughes T.P., Kerry J.T., Baird A.H., Connolly S.R., Dietzel A., Eakin C.M., Heron S.F., Hoey A.S., Hoogenboom M.O., Liu G., McWilliam M.J., Pears R.J., Pratchett M.S., Skirving W.J., Stella J.S. & Torda G. (2018b). Global warming transforms coral reef assemblages. Nature, 556, 492-+.

Hughes, T.P., Kerry, J.T., Baird, A.H., Connolly, S.R., Chase, T.J., Dietzel, A., Hill, T., Hoey, A.S., Hoogenboom, M.O., Jacobson, M. & Kerswell, A., (2019a). Global warming impairs stock–recruitment dynamics of corals. Nature, 568(7752), pp.387-390.

Hughes, T.P., Kerry, J.T., Connolly, S.R., Baird, A.H., Eakin, C.M., Heron, S.F., Hoey, A.S., Hoogenboom, M.O., Jacobson, M., Liu, G. and Pratchett, M.S., (2019b). Ecological memory modifies the cumulative impact of recurrent climate extremes. *Nature Climate Change*, *9*(1), pp.40-43.

Ishwaran H. (2015) The effect of splitting on random forests. Machine Learning, 99, 75-188.

Kayanne, H. Validation of degree heating weeks as a coral bleaching index in the northwestern Pacific. Coral Reefs 36, 63–70 (2017). https://doi.org/10.1007/s00338-016-1524-y

Kumagai NH, Yamano H, Committee Sango-Map-Project. (2018). High-resolution modeling of thermal thresholds and environmental influences on coral bleaching for local and regional reef management. PeerJ 6:e4382 https://doi.org/10.7717/peerj.4382

Lawrey, E. P., Stewart M. (2016) Mapping the Torres Strait Reef and Island Features - Extending the GBR Features (GBRMPA) dataset. Report to the National Environmental Science Programme. Reef and Rainforest Research Centre Limited, Cairns (117pp.).

Liaw, A. Wiener, M. (2002). Classification and Regression by randomForest. R News 2(3), 18—22.

Li, J. (2011). Novel spatial interpolation methods for environmental properties: using point samples of mud content as an example. *The Survey Statistician: The Newsletter of the International Association of Survey Statisticians*, (63), 15-16.

Li, J., Potter, A., Huang, Z., & Heap, A. (2012). Predicting Seabed Sand Content across the Australian Margin Using Machine Learning and Geostatistical Methods (p. 115). Geoscience Australia.

Li, J., Alvarez, B., Siwabessy, J., Tran, M., Huang, Z., Przeslawski, R., Radke, L., Howard, F. and Nichol, S., (2017). Application of random forest, generalised linear model and their hybrid methods with geostatistical techniques to count data: Predicting sponge species richness. *Environmental modelling & software*, *97*, pp.112-129.

Liu, G., A.E. Strong, and W. Skirving. (2003). Remote sensing of sea surface temperature during 2002 Barrier Reef coral bleaching. EOS, 84 (15), 137-144.

Liu, G., Heron, S.F., Eakin, C.M., Muller-Karger, F.E., Vega-Rodriguez, M., Guild, L.S., De La Cour, J.L., Geiger, E.F., Skirving, W.J., Burgess, T.F.R., Strong, A.E., Harris, A., Maturi, E., Ignatov, A., Sapper, J., Li, J. and Lynds, S., (2014). Reef-Scale Thermal Stress Monitoring of Coral Ecosystems: New 5-km Global Products from NOAA Coral Reef Watch. Remote Sens., 6, 11579-11606.

Meinshausen, N. (2006). Quantile regression forests. Journal of Machine Learning Research, 7(Jun), 983-999.

Meinshausen, N. (2017). quantregForest: Quantile Regression Forests. R package version 1.3-7. https://CRAN.R-project.org/package=quantregForest

Mellin, C., Matthews, S., Anthony, K.R., Brown, S.C., Caley, M.J., Johns, K.A., Osborne, K., Puotinen, M., Thompson, A., Wolff, N.H. and Fordham, D.A., (2019a). Spatial resilience of the Great Barrier Reef under cumulative disturbance impacts. Global change biology, 25(7), pp.2431-2445.

Mellin, C., Thompson, A., Jonker, M. J., and Emslie, M. J. (2019b). Cross-shelf variation in coral community response to disturbance on the Great Barrier Reef. Diversity 11: 38.

R Core Team (2020). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL: https://www.R-project.org

Reaser, J. K., Pomerance, R., & Thomas, P. O. (2000). Coral bleaching and global climate change: scientific findings and policy recommendations. Conservation biology, 14(5), 1500-1511

Shan, Y., Paull, D., & McKay, R. I. (2006). Machine learning of poorly predictable ecological data. *Ecological Modelling*, *195*(1-2), 129-138.

Sinnott, R.W, 1984. Virtues of the Haversine. Sky and Telescope 68(2): 159

Strong, A.E., C.S. Barrientos, C. Duda, and J. Sapper. (1997). Improved satellite techniques for monitoring coral reef bleaching, Proc 8th Int'l Coral Reef Sym, 2, 1495-1498.

Strong, A.E., G. Liu and R. Brainard, 2003. NOAA Satellites Give Early Warning for Coral Bleaching in the Northwestern Hawaii Archipelago. Coastlines. 13 (3), 8-11.

Westcott, D.A., Fletcher, C.S., Kroon, F.J., Babcock, R.C., Plagányi, E.E., Pratchett, M.S., Bonin, M.C. (2020). Relative efficacy of three approaches to mitigate Crown-of-Thorns Starfish outbreaks on Australia's Great Barrier Reef. *Scientific Reports.* **10,** 12594

Wikle, C. K., & Berliner, L. M. (2007). A Bayesian tutorial for data assimilation. Physica D: Nonlinear Phenomena, 230(1-2), 1-16.

Wilkinson, C. (2008). Status of coral reefs of the world: 2008. Global Coral Reef Monitoring Network and Reef and Rainforest Research Centre, Townsville, Australia, 296 p.

APPENDIX 1: SCATTERPLOTS OF DATA

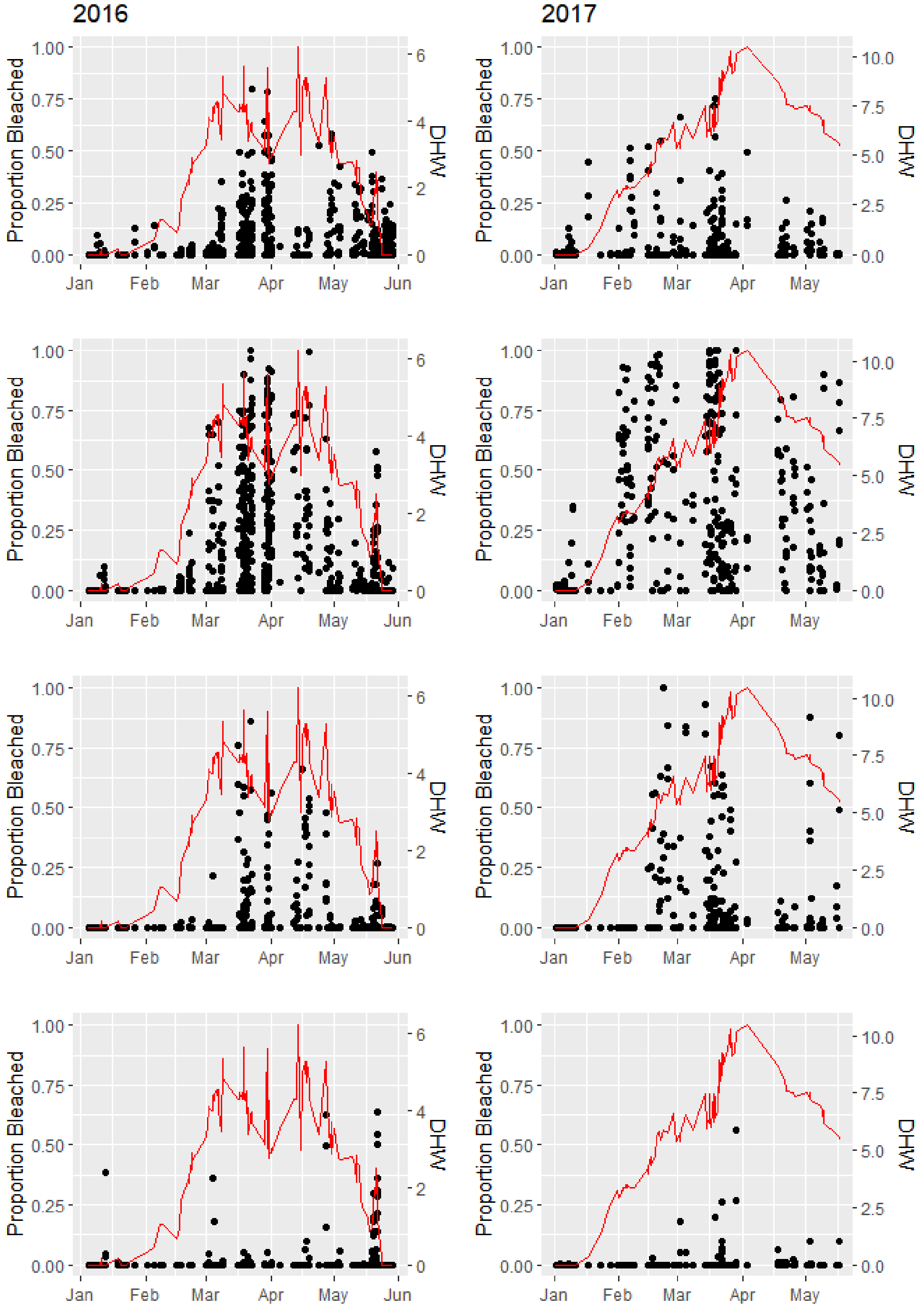

Figure A.1: Plots showing bleached proportion (black points) and DHWcurrent (red line) vs day for 2016 (left) and 2017 (right) bleaching season. Top row shows severity category 1, row 2 shows severity category 2, row 3 shows severity category 3, and row 4 shows severity category 4.

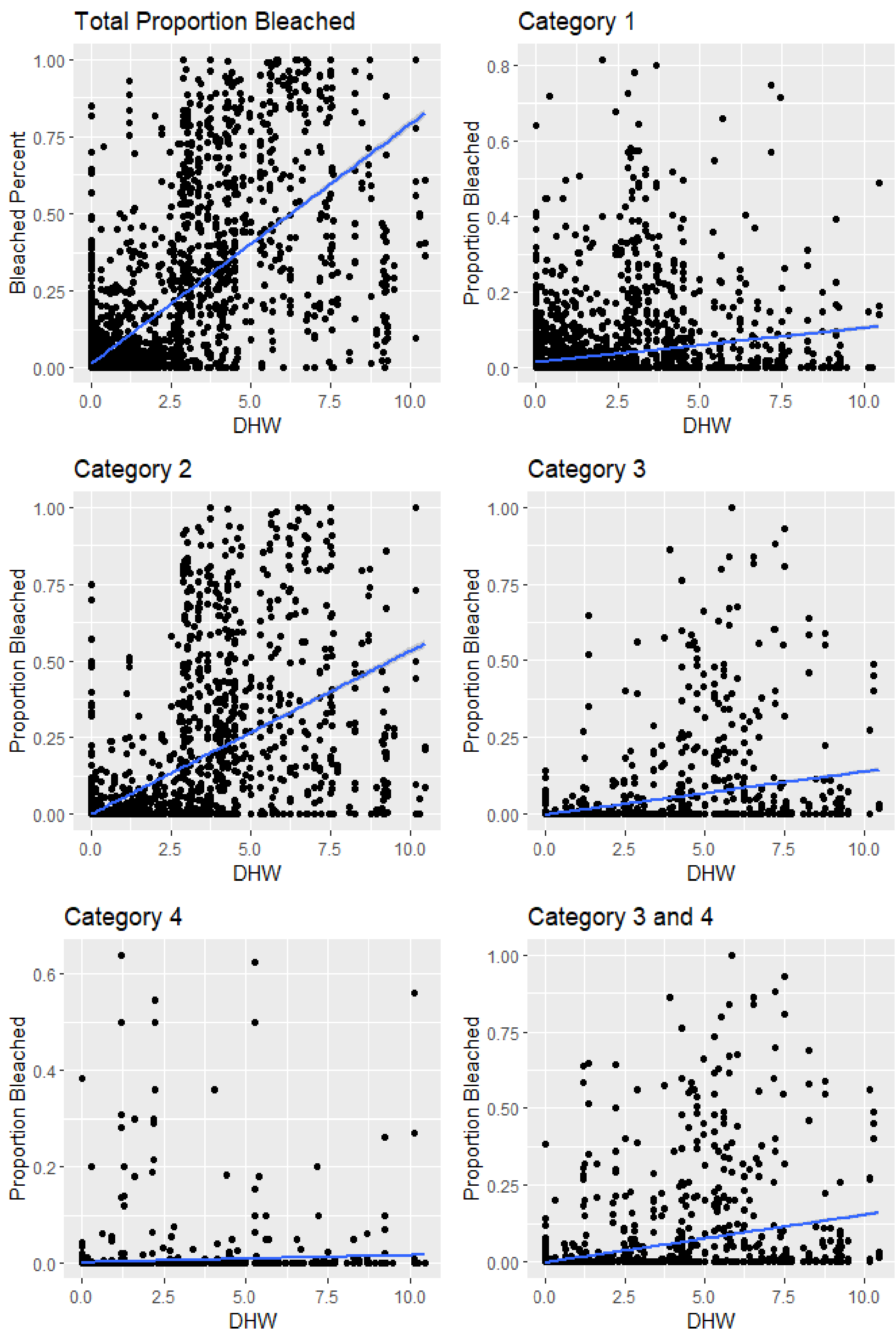

Figure A.2: Scatterplots of proportion bleaching vs degree heating weeks. A linear fit is in blue.

APPENDIX 2: TABLES BY DHW CATEGORIES

This section presents tables for estimates of the total area bleached by severity category, total bleached, and proportion of recently dead coral for 2016 and 2017, divided according to different DHW categories. The DHW categories are DHW less than 1, DHW 1-4, DHW 4-8, and DHW greater than 8.

Tables for 2016

Table A.1: Total area bleached, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	839.3851	0.168	0.000	0.620
1-4	7309.784	2025.4245	0.277	0.004	0.716
4-8	6695.289	4213.7492	0.629	0.142	0.936
>8	9449.351	5024.2276	0.532	0.197	0.912

Table A.2: Area bleached in category 1 severity, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	304.6391	0.061	0	0.327
1-4	7309.784	553.9607	0.076	0	0.386
4-8	6695.289	391.7861	0.059	0	0.342
>8	9449.351	810.3737	0.086	0	0.267

Table A.3: Area bleached in category 2 severity, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	563.9481	0.113	0.000	0.517
1-4	7309.784	1126.0504	0.154	0.000	0.574
4-8	6695.289	2862.6640	0.428	0.004	0.892
>8	9449.351	3115.5888	0.330	0.000	0.872

Table A.4: Area bleached in category 3 severity, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	15.46963	0.003	0	0.054
1-4	7309.784	80.88289	0.011	0	0.067
4-8	6695.289	1063.13531	0.159	0	0.463
>8	9449.351	1203.58531	0.127	0	0.569

Table A.5: Area bleached in category 4 severity, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	3.448598	0.001	0	0.002
1-4	7309.784	28.001761	0.004	0	0.027
4-8	6695.289	73.427477	0.011	0	0.102
>8	9449.351	168.913321	0.018	0	0.149

Table A.6: Area bleached in category 3 or 4 severity, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	5001.162	18.50378	0.004	0	0.040
1-4	7309.784	85.88850	0.012	0	0.088
4-8	6695.289	1096.57433	0.164	0	0.493
>8	9449.351	1580.21965	0.167	0	0.580

Table A.7: Area recently dead coral, divided by DHW groupings, for 2016.

DHW	AREA (KM^2)	AREA RDC	PROPORTION RDC	LOWER BOUND	UPPER BOUND
<1	5001.162	150.5102	0.030	0.000	0.150
1-4	7309.784	215.7913	0.030	0.000	0.136
4-8	6695.289	423.5309	0.063	0.000	0.301
>8	9449.351	1190.6334	0.126	0.024	0.265

Tables for 2017

Table A.8: Total area bleached, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	208.8432	0.198	0.000	0.727
1-4	9412.696	2408.8968	0.256	0.012	0.663
4-8	11212.034	7028.9102	0.627	0.171	0.918
>8	6776.719	3534.5280	0.522	0.204	0.873

Table A.9: Area bleached in category 1 severity, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	67.19275	0.064	0	0.350
1-4	9412.696	1137.50035	0.121	0	0.424
4-8	11212.034	536.13946	0.048	0	0.259
>8	6776.719	753.87843	0.111	0	0.301

Table A.10: Area bleached in category 2 severity, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	133.7166	0.127	0.000	0.611
1-4	9412.696	1129.9750	0.120	0.002	0.485
4-8	11212.034	4526.5535	0.404	0.001	0.852
>8	6776.719	1922.7521	0.284	0.000	0.799

Table A.11: Area bleached in category 3 severity, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	3.791223	0.004	0	0.065
1-4	9412.696	102.606162	0.011	0	0.077
4-8	11212.034	2132.246779	0.190	0	0.519
>8	6776.719	923.478738	0.136	0	0.546

Table A.12: Area bleached in category 4 severity, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	0.4777529	0.000	0	0.007
1-4	9412.696	27.1074597	0.003	0	0.018
4-8	11212.034	209.8772757	0.019	0	0.130
>8	6776.719	65.0601222	0.010	0	0.086

Table A.13: Area bleached in category 3 or 4 severity, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA BLEACHED	PROPORTION BLEACHED	LOWER BOUND	UPPER BOUND
<1	1054.138	31.06481	0.029	0.000	0.126
1-4	9412.696	224.03609	0.024	0.000	0.085
4-8	11212.034	763.38918	0.068	0.000	0.291
>8	6776.719	770.98641	0.114	0.026	0.230

Table A.14: Area recently dead coral, divided by DHW groupings, for 2017.

DHW	AREA (KM^2)	AREA RDC	PROPORTION RDC	LOWER BOUND	UPPER BOUND
<1	1054.138	45.60615	0.043	0.013	0.154
1-4	9412.696	342.35360	0.036	0.012	0.109
4-8	11212.034	1174.56537	0.105	0.020	0.303
>8	6776.719	690.45925	0.102	0.032	0.226

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