

NOTE

# A decline in bleaching suggests that depth can provide a refuge from global warming in most coral taxa

Andrew H. Baird<sup>1,\*</sup>, Joshua S. Madin<sup>2</sup>, Mariana Álvarez-Noriega<sup>1,3</sup>,  
Luisa Fontoura<sup>4</sup>, James T. Kerry<sup>1</sup>, Chao-Yang Kuo<sup>1,5</sup>, Kristin Precoda<sup>2</sup>,  
Damaris Torres-Pulliza<sup>4</sup>, Rachael M. Woods<sup>4</sup>, Kyle J. A. Zawada<sup>4,6</sup>, Terry P. Hughes<sup>1</sup>

<sup>1</sup>Australian Research Council Centre of Excellence for Coral Reef Studies, James Cook University, Townsville, QLD 4811, Australia

<sup>2</sup>Hawai'i Institute of Marine Biology, School of Ocean and Earth Science and Technology, University of Hawai'i, Kāne'ohe, HI 96744, USA

<sup>3</sup>College of Marine & Environmental Sciences, James Cook University, Townsville, QLD 4811, Australia

<sup>4</sup>Department of Biological Sciences, Macquarie University, Sydney, NSW 2109, Australia

<sup>5</sup>Biodiversity Research Center, Academia Sinica, Nankang, Taipei 11529, Taiwan

<sup>6</sup>Centre for Biological Diversity, Scottish Oceans Institute, University of St. Andrews, St. Andrews KY16 9TH, Scotland, UK

**ABSTRACT:** Coral reefs are under increasing threat from increasing warm temperature stress. Coral bleaching is caused by a combination of heat and light anomalies and therefore fewer corals should bleach in areas where either heat or light anomalies are ameliorated, such as in turbid waters or at depth. Here, we explore the overall response of the coral assemblage and of 16 individual taxa to a thermal anomaly along a depth gradient during the 2016 mass bleaching event at sites on the outer shelf of the northern Great Barrier Reef. Across all taxa, there was a curvilinear decline in the percentage of colonies bleached with depth that was consistent among sites and reflected the attenuation of light in the ocean. The percentage of colonies bleached was also higher on reefs with higher levels of temperature stress. In 10 taxa, including the abundant and ecologically significant *Acropora*, *Pocillopora* and *Porites*, the percentage of colonies bleached declined with depth. In 4 taxa, the percentage of colonies bleached peaked at intermediate depth. In 2 taxa, there was no effect of depth because bleaching was uniformly low. These data suggest that deeper areas of reef can provide a refuge from mass bleaching for many colonies of most taxa.

**KEY WORDS:** Climate change · Global warming · Coral reefs · Depth zonation · Disturbance · Recovery

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## INTRODUCTION

The world's tropical reef systems are increasingly affected by warming and variable temperatures (Hughes et al. 2003, 2018b, Spalding & Brown 2015). In 2015–2016, record high temperatures triggered the third global-scale coral bleaching event (Hughes et al. 2018a) since mass bleaching was first docu-

mented in the 1980s (Glynn 1984). The Great Barrier Reef (GBR) was one of the worst affected regions during the 2016 event: 91% of the reefs on the world's largest reef system were bleached to some extent, and the proportion of reefs with >60% of corals bleached was 4 times higher than in any previous event on the GBR (Hughes et al. 2017). Projected increases in the frequency and severity of coral bleach-

ing in the near future (Donner 2009) mean that there is an urgent need to better understand the ecology of the phenomenon—in particular, to identify areas that might act as potential refuges from mass bleaching (Riegl & Piller 2003, McClanahan et al. 2009, Cacciapaglia & van Woesik 2015).

The severity of coral bleaching varies among locations due to both ecological and environmental factors (McClanahan et al. 2018). For example, the proportion of the assemblage affected by bleaching is influenced by coral assemblage structure (Marshall & Baird 2000, McClanahan et al. 2005), and higher temperature stress generally results in a higher proportion of colonies that bleach (Kleypas et al. 2008, Hughes et al. 2017). Coral bleaching, defined as the loss of the obligate symbiotic dinoflagellate from the cells of the coral host, is a generalised stress response with numerous causes, including sedimentation, freshwater exposure or disease (Brown 1997, Baird et al. 2009). However, the most geographically extensive and severe events are triggered by sustained periods of elevated sea water temperatures (Goreau 1999, McClanahan et al. 2007, Eakin et al. 2010). Thermal bleaching is caused by the combination of heat and light (Lesser 1997, Takahashi et al. 2004), and therefore refuges from bleaching are likely to occur where oceanographic or atmospheric conditions reduce sea water temperature anomalies or light irradiance (Glynn 1996, Riegl & Piller 2003, West & Salm 2003, Cacciapaglia & van Woesik 2016).

Light intensity attenuates predictably with depth (Lesser 1997, Lesser et al. 2009), and while the attenuation of temperature with depth is much more variable (Bongaerts et al. 2010), temperatures are on occasion lower in deeper reef areas (Smith et al. 2014, Prasetya et al. 2016). Therefore, the incidence of bleaching and subsequent mortality are expected to be lower at greater depths (Glynn 1996). Consistent with this expectation, bleaching and mortality are typically lower at greater depths (Glynn et al. 2001, Muir et al. 2017). For example, mortality rates of corals at a depth of 6 m were only a third of those in 2 m across several turbid inshore reefs on the GBR in 1998 (Marshall & Baird 2000). Similarly, a transition from high to low mortality was observed below 8–15 m at numerous sites in the western Indian Ocean during 1998 (Sheppard & Obura 2005). In the bleaching event of 2015–2016, 73% of species at sites in the Maldives had individuals at 24–30 m that were not affected by bleaching (Muir et al. 2017). However, bleaching and mortality do not always decline with depth. For example, there was a large but equal loss of coral cover between 2 and 10 m following

bleaching in the Maldives in 1998 (McClanahan 2000). In addition, the proportion of the coral assemblage bleached was higher at 12 and 18 m than at 6 m in Moorea, a finding attributed to higher flow and wave energy in the shallows (Penin et al. 2007). Nonetheless, neither of these 2 studies sampled over the complete depth range of the coral assemblage, and therefore it is possible that bleaching or mortality were lower at greater depths. In addition, few studies look in detail at patterns of bleaching with depth among different taxa (but see Bridge et al. 2014, Muir et al. 2017).

The aims of the present study were to test whether or not depth could serve as a refuge from bleaching across a depth gradient from 2 to 27 m at 11 sites on the outer edge of the northern GBR during a large-scale coral bleaching event in 2016. We show that the overall percentage of colonies that bleached declined rapidly with depth with a similar result in 10 of the 16 taxa examined. We conclude that depth did serve as a refuge for many colonies of most taxa, providing a potential source of recruits for recolonisation of the shallows in the future.

## MATERIALS AND METHODS

We conducted in-water surveys at 11 sites on 7 reefs between 11 and 14 April 2016 (Fig. 1) on the outer edge of the northern GBR, from 11° to 13° S, 4 wk after the peak in seawater temperatures in March (Hughes et al. 2017). Sites were chosen haphazardly depending on the wind, swell, tide and time of day. All sites had uniform water clarity with horizontal visibility of approximately 20–30 m. Two survey methods were used. Surveys at 2 m consisted of five 10 × 1 m belt transects (following Hughes et al. 2017, 2018b). Surveys at 7, 12, 17, 22 and 27 m consisted of 5 replicate 1 m<sup>2</sup> virtual quadrats (following McClanahan et al. 2004), by each of 3 observers (A.H.B., C.-Y.K. and M.A.N.). The 5 quadrats from each observer were then pooled to produce 3 replicate estimates of bleaching at each depth below 2 m (i.e. 1 replicate for each observer). All surveys were on surfaces exposed to direct light, and therefore colonies were neither shaded by overhangs nor other bathymetric features. Every scleractinian colony in the quadrats was identified to genus and these plus all soft corals were assigned a categorical bleaching score as follows: (1) no bleaching, (2) slight paling compared to normal coloration, (3) 1–50% of colony bleached, (4) 51–99% of colony bleached, (5) 100% of colony bleached, or (6) recently dead.

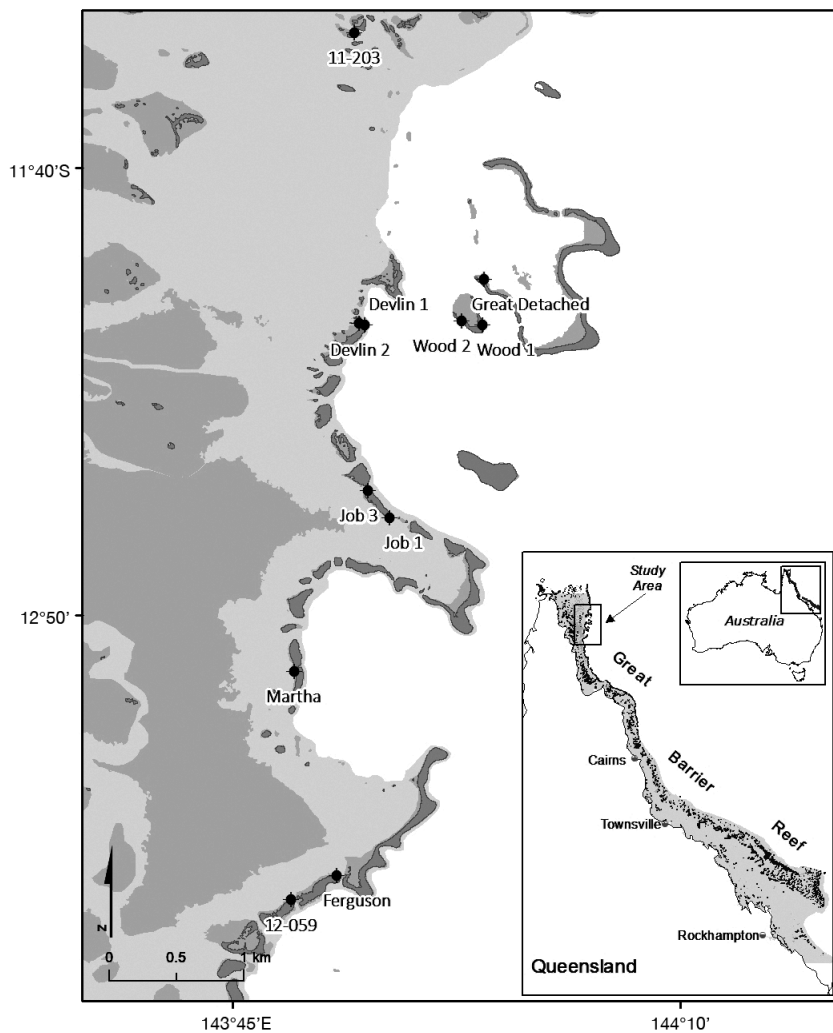


Fig. 1. Study sites in the northern Great Barrier Reef (inset: Great Barrier Reef; smaller inset: Australia)

To analyse the relationship between the overall extent of bleaching with depth, we used a generalised linear mixed effect model with a binary response variable (0: unbleached [bleaching category 1] and 1: bleached [bleaching categories 2–6]). Fixed effects were the depth of assemblages, the square of depth (i.e. to allow for monotonic and quadratic trends), and the maximum degree heating weeks (DHW) experienced by the 7 reefs during the 2016 bleaching event. Depth was  $\log_{10}$ -transformed to improve model residuals. Satellite-derived DHW values were calculated using the Optimum Interpolation Sea Surface Temperature (Reynolds et al. 2007) with the period 1985–2012 as a baseline (Heron et al. 2015). We considered the interaction between the depth variables and DHW to allow depth trends to vary among reefs. We included random effects for site and genus to account

for and explore variation caused by differences among 10 sites and 47 genera. The variation associated with taxa was over an order of magnitude greater than the variation associated with sites, suggesting that taxon-specific differences in responses to bleaching with depth were important (Table 1, Fig. S1 at [www.int-res.com/articles/suppl/m603p257\\_supp.pdf](http://www.int-res.com/articles/suppl/m603p257_supp.pdf)). Therefore, we tested bleaching by depth patterns individually among the 16 taxa that had  $\geq 90$  observations across the entire dataset. Taxon models included the same fixed factors (depth, depth squared and DHW) and site as a random effect. All analyses were run using the 'glmer' function with a binomial link response in the package 'lme4' (Bates et al. 2015) in R (R Core Team 2018). Models were selected based on 'AIC' and 'BIC' functions in R, where best models had information criterion values 2 units below competing models (Table S1 in the Supplement). The 'r.squaredGLMM' function in the 'MuMIn' package in R was used to calculate conditional (both fixed and random effects) and marginal (fixed effects only)  $r^2$  coefficients (Barton 2018). The relative importance of explanatory variables (i.e. percent of explained variance) was calculated by hierarchical partitioning using the R package 'hier.part' (Walsh & MacNally 2013).

## RESULTS AND DISCUSSION

Overall, the percentage of colonies that bleached declined with depth and was greater on reefs that experienced higher DHW (Fig. 2). The lack of a significant interaction between depth and DHW indicates that the shape of the bleaching by depth curve was consistent among sites (Table 1). The decline in bleaching with depth was curvilinear, such that the attenuation over the first few metres was much larger than at greater depths. For example, the proportion of bleached colonies at 12 m was approximately 50% lower than at 2 m, whereas between 12 and 27 m, bleaching only declined by a further 20% (Fig. 2). The attenuation of light with depth in the ocean is also curvilinear (Lesser et al. 2009), suggesting that

Table 1. Best-fit model results for bleaching in the overall assemblage showing random effect variance and fixed effect parameter estimates. \*\*\*Pr < 0.001 and \*\*Pr < 0.01. Marginal and conditional  $r^2$  values are 0.17 and 0.46, respectively. The independent effects (IE) value corresponds to the percentage of the explained variance accounted for by each explanatory variable. DHW: degree heating weeks

Random effects	Variance	SD			
Taxa (intercept)	1.998	1.414			
Site (intercept)	0.132	0.363			
Fixed effects	Estimate	SE	z-value	Pr(> z )	IE (%)
(Intercept)	-2.291	0.854	-2.683	0.007**	
Depth	-2.285	0.074	-30.939	<0.001***	81.5
DHW	0.384	0.107	3.607	<0.001***	18.5

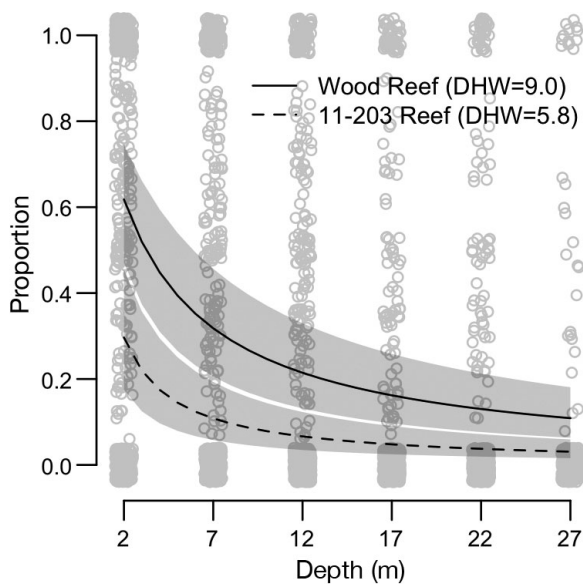


Fig. 2. Proportion of corals bleached as a function of depth in the total coral assemblage. Lines are the best model fits ( $\pm 95\%$  confidence intervals) for the reefs with the highest (black solid) and lowest (black dashed) degree heating weeks (DHW,  $^{\circ}\text{C}$ -weeks) and the overall best fit model (white solid) recorded during the 2016 bleaching event

this might be an important cause of the observed decline in bleaching with depth. A similar reduction in bleaching is often produced by shading, where colonies in microhabitats that offer some protection from sunlight bleach less than colonies of the same species in the open (e.g. Hoogenboom et al. 2017, Muir et al. 2017).

Despite the importance of depth and DHW for predicting the proportion of bleached coral in the overall assemblage, these 2 variables only explained 17% of the variation (Table 1). The random effects—i.e. unobserved site variation and the taxonomic composition

of the coral assemblages—increased the total variation explained to 50% (Table 1). Most of this variation was attributable to taxa (Table 1), suggesting that sites or depths with a greater proportion of susceptible taxa bleached more readily. Nonetheless, this still leaves 50% of the variation in bleaching unaccounted for, indicating that factors other than those associated with depth, site and taxa are influencing these bleaching patterns.

The percentage of colonies that bleached varied among depths in 14 of the 16 taxa (Fig. 3, Table 2). In 10 taxa, there was a monotonic decline in bleaching with depth: *Acropora*, *Pocillopora*, *Porites*, *Stylophora*, *Goniastrea*, *Isopora*, *Dispastraea*, *Favites*, *Cyphastrea*

and *Platygyra* (Fig. 3, Table 2). In 4 taxa, the pattern was hump-shaped, with maximum (*Montipora*, soft corals and *Pavona*), or minimum (*Seriatopora*) bleaching occurring at intermediate depths (Fig. 3, Table 2). In 2 genera, *Echinopora* and *Lobophyllia*, was there no relationship with depth because bleaching was uniformly low (Fig. 3, Table 2). In general, bleaching decreased most dramatically over a fairly narrow depth range. For example, the percentage of bleached colonies of *Acropora* at 12 m was half that at 2 m (Fig. 3), and very few *Porites* colonies were bleached below 7 m (Fig. 3). DHW was important for 9 of the 16 taxa, with the proportion of colonies bleached higher on reefs with higher DHW (Fig. 3, Table 2). The percentage of variation explained by the models ranged from 3% in *Cyphastrea* to 62% in *Pavona*, suggesting that other factors, such as species identity, are also driving the bleaching patterns. Nonetheless, depth did provide a refuge for a large number of colonies in most taxa on these reefs, substantiating similar findings in Indonesia (Bridge et al. 2014), the eastern Pacific (Smith et al. 2014) and the Maldives (Muir et al. 2017).

The suggestion that depth can provide a refuge from bleaching is an issue of some controversy (Smith et al. 2016). Lower reproductive output at depth (Shlesinger et al. 2018) and low levels of genetic connectivity between deep and shallow populations has led some to question the capacity of deep populations to successfully seed shallow areas of reef (Bongaerts et al. 2017). However, while such factors might limit dispersal between deep and shallow populations, they will not prevent it. Furthermore, a transition from high to low mortality generally occurs at depths of between 4 and 8 m (Bridge et al. 2014, our Figs. 2 & 3), a depth range over which neither differences in reproductive output nor distance are likely to inhibit dispersal. Indeed, in all but 4 of our 16 taxa, the pro-

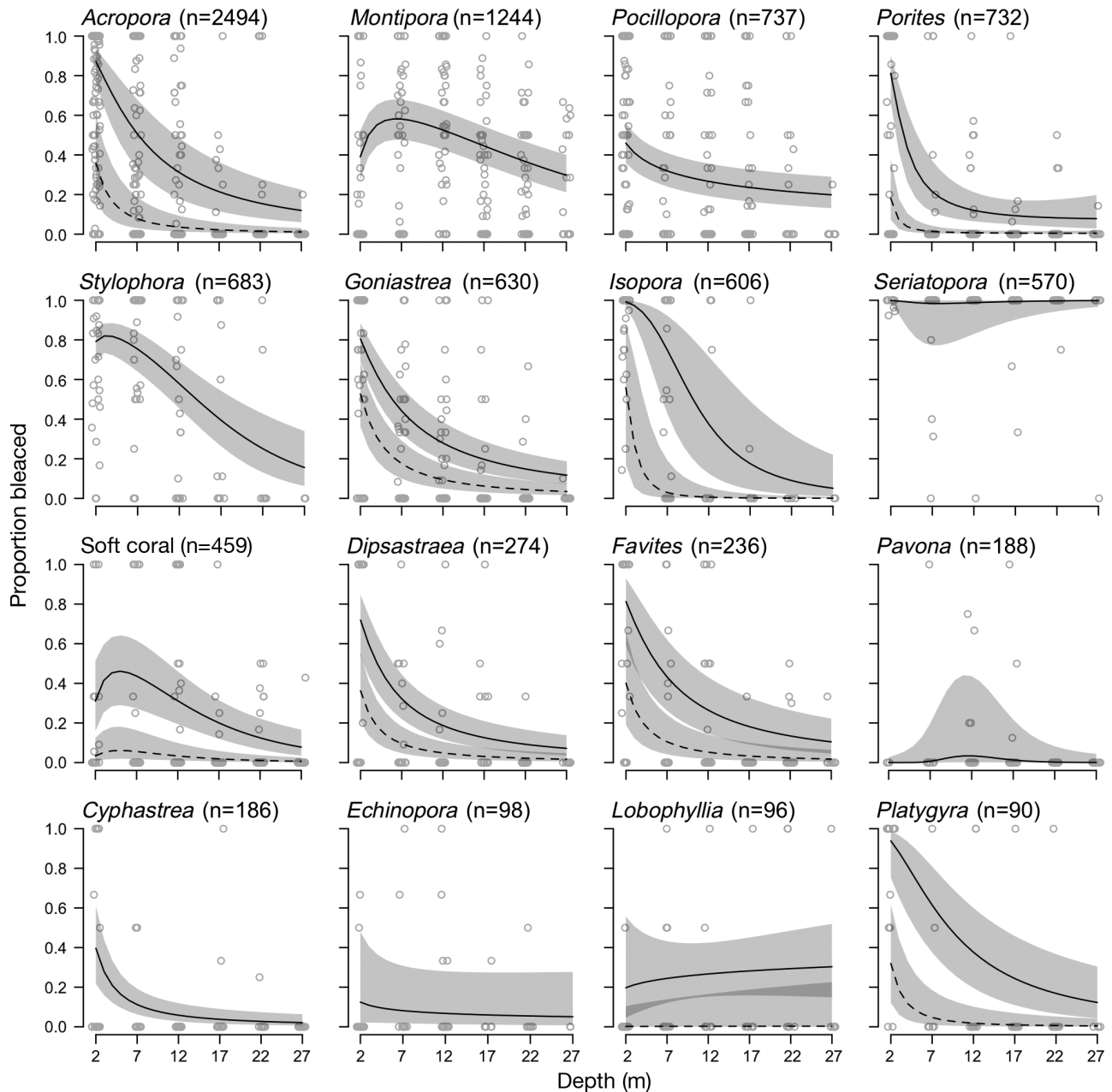


Fig. 3. Proportion of corals bleached as a function of depth for genera with  $\geq 90$  observations. Panels with solid and dashed lines reflect a significant effect of degree heating weeks (DHW) and lines reflect the maximum and minimum DHW in the dataset. Panels with a single solid line reflect only significant depth effects. Shaded areas are 95% confidence intervals for fixed component of best fit models. See Table 2 for models

portion of colonies bleached at 12 m was lower than at 2 m (Fig. 3).

In conclusion, these data suggest that deeper areas of the outer-edge reefs on the GBR provided a refuge from the 2016 bleaching event for some colonies of most taxa, in particular, abundant and ecologically significant taxa such as *Acropora*, *Pocillopora* and *Porites*. However, closer to shore, very few reefs support corals at these depths. Indeed, most inner- and

mid-shelf reefs within the GBR lagoon bottom out onto sand between 5 and 15 m. In addition, the outer-edge reefs are close to deeper cooler waters and are generally unaffected by land-based nutrients: factors that can potentially reduce bleaching (Done et al. 2003, Wiedenmann et al. 2013). Consequently, the refuge from bleaching provided by depth on these outer-edge reefs is not necessarily going to be replicated throughout most of the GBR.



Table 2. Best models for the 16 coral genera with  $\geq 90$  observations ranked from most to least abundant (see Fig. 3). \*\*\*Pr < 0.001, \*\*Pr < 0.01 and \*Pr < 0.05. Marginal (m) and conditional (c)  $r^2$  values are given in parentheses. The independent effects (IE) value corresponds to the percentage of the explained variance accounted for by each explanatory variable. DHW: degree heating weeks

Genus	Parameter	Estimate	SE	z-value	Pr(> z )	IE (%)
<i>Acropora</i> (m = 0.38, c = 0.46)	(Intercept)	-3.471	1.622	-2.140	0.032*	
	Depth	-3.463	0.163	-21.309	<0.001***	49.1
	DHW	0.715	0.211	3.387	<0.001***	50.9
<i>Montipora</i> (m = 0.05, c = 0.10)	(Intercept)	-1.650	0.457	-3.612	<0.001***	
	Depth	4.915	1.000	4.913	<0.001***	44.5
	Depth squared	-3.048	0.561	-5.437	<0.001***	55.5
<i>Pocillopora</i> (m = 0.08, c = 0.16)	(Intercept)	0.164	0.243	0.675	0.499	
	Depth	-1.088	0.211	-5.154	<0.001***	100.0
<i>Porites</i> (m = 0.34, c = 0.34)	(Intercept)	-3.984	1.714	-2.324	0.020*	
	Depth	-8.142	2.109	-3.860	<0.001***	43.2
	Depth squared	2.693	1.366	1.971	0.049*	40.3
	DHW	0.850	0.212	4.013	<0.001***	16.5
<i>Stylophora</i> (m = 0.16, c = 0.22)	(Intercept)	0.464	0.528	0.880	0.379	
	Depth	4.062	1.701	2.387	0.017*	42.6
	Depth squared	-3.890	1.167	-3.333	<0.001***	57.4
<i>Goniastrea</i> (m = 0.36, c = 0.36)	(Intercept)	-1.043	1.041	-1.002	0.316	
	Depth	-3.042	0.294	-10.357	<0.001***	52.1
	DHW	0.375	0.138	2.729	0.006**	47.9
<i>Isopora</i> (m = 0.61, c = 0.68)	(Intercept)	-4.914	3.054	-1.609	0.108	
	Depth	-6.856	0.761	-9.014	<0.001***	50.1
	DHW	1.311	0.413	3.175	0.001**	49.9
<i>Seriatopora</i> (m = 0.00, c = 0.06)	(Intercept)	10.694	1.998	5.352	<0.001***	
	Depth	-14.849	3.534	-4.202	<0.001***	49.0
	Depth squared	8.346	2.240	3.725	<0.001***	51.0
Soft coral (m = 0.22, c = 0.22)	(Intercept)	-8.806	2.077	-4.240	<0.001***	
	Depth	5.857	2.156	2.717	0.007**	17.8
	Depth squared	-4.234	1.284	-3.297	<0.001***	25.5
	DHW	0.736	0.219	3.359	<0.001***	56.7
<i>Dipsastraea</i> (m = 0.32, c = 0.32)	(Intercept)	-1.997	1.170	-1.706	0.088	
	Depth	-3.097	0.489	-6.329	<0.001***	51.9
	DHW	0.430	0.155	2.777	0.005**	48.1
<i>Favites</i> (m = 0.31, c = 0.32)	(Intercept)	-2.382	1.588	-1.500	0.134	
	Depth	-3.199	0.599	-5.345	<0.001***	47.7
	DHW	0.535	0.215	2.484	0.013*	52.3
<i>Pavona</i> (m = 0.62, c = 0.78)	(Intercept)	-43.565	19.982	-2.180	0.029*	0.0
	Depth	75.580	37.361	2.023	0.043*	44.4
	Depth squared	-35.506	17.357	-2.046	0.041*	55.6
<i>Cyphastrea</i> (m = 0.03, c = 0.03)	(Intercept)	0.491	0.612	0.802	0.422	
	Depth	-3.033	0.716	-4.236	<0.001***	100.0
<i>Echinopora</i> (m = 0.02, c = 0.36)	(Intercept)	-1.691	1.123	-1.505	0.132	
	Depth	-0.866	0.939	-0.922	0.356	100.0
<i>Lobophyllia</i> (m = 0.03, c = 0.03)	(Intercept)	-14.430	5.768	-2.502	0.012*	
	Depth	0.505	0.924	0.547	0.585	56.4
	DHW	1.430	0.675	2.118	0.034*	43.6
<i>Platygyra</i> (m = 0.56, c = 0.56)	(Intercept)	-4.977	2.103	-2.366	0.018*	
	Depth	-4.150	0.911	-4.553	<0.001***	51.0
	DHW	0.995	0.316	3.150	0.002**	49.0

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