Differential bleaching susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia's Great Barrier Reef and Coral Sea Marine Parks

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A B S T R A C T

Climate-induced coral bleaching represents the foremost threat to coral assemblages globally, however bleaching susceptibility varies among and within coral taxa. We compared bleaching susceptibility among 10 coral morpho-taxa and two colony size classes relative to reef-scale bleaching severity at 33 reefs across the Great Barrier Reef and Coral Sea Marine Parks in February–March 2020. Colony size and bleaching severity caused the hierarchy of bleaching susceptibility among taxa to change considerably. Notably, massive *Porites* shifted from being among the least likely taxa to exhibit bleaching, to among the most susceptible as overall bleaching severity increased. Juvenile corals (≤5 cm diameter) were generally more resistant to bleaching, except for *Montipora* and *Pocillopora* colonies, which were more likely to bleach than adults (>5 cm). These findings suggest that colony size and reef-scale bleaching severity are important determinants of bleaching susceptibility among taxa and provide insights into possible shifts in the structure of coral assemblages caused by bleaching events.

1. Introduction

Anthropogenic climate change is leading to increased incidence and severity of marine heatwaves (Hobday et al., 2016; Oliver et al., 2018; Skirving et al., 2019), which on coral reefs, is directly linked to widespread mass coral bleaching and mortality (Hughes et al., 2017; Hughes et al., 2018a; Skirving et al., 2019). Prolonged exposure to elevated temperatures and/or extreme short-term increases in temperature can disrupt the symbiotic relationship between corals and zooxanthellae (Symbiodiniaceae), resulting in declines in intracellular densities or performance of zooxanthellae. Such declines in the densities of zooxanthallae cause the coral to appear pale or white (bleached), and greatly constrain the capacity of the coral host to obtain energy (Glynn, 1984; Douglas, 2003). The frequency and severity of marine heatwaves and corresponding mass-bleaching episodes has increased markedly in the last few decades (Oliver et al., 2018; Hughes et al., 2018a; Hughes et al., 2019b) and is predicted to continue to increase under ongoing climate change (van Hooidonk et al., 2013; Skirving et al., 2019; Li and Donner, 2022).

Coral taxa are widely reported to vary in their bleaching susceptibility (e.g., Baskin, 1998; Loya et al., 2001). Generally, fast growing and finely branched corals (e.g., *Stylophora* and *Acropora*) are most susceptible to bleaching, whereby a very large proportion of colonies (approaching 100 %) exhibit bleaching (Marshall and Baird, 2000; Baird and Marshall, 2002; Pratchett et al., 2013; Hughes et al., 2017; Harrison et al., 2018; McClanahan et al., 2020) and high levels of mortality (Brown and Suharsono, 1990; Fujioka, 1999; Loya et al., 2001; Baird and Marshall, 2002). In contrast, coral taxa with massive and encrusting morphologies (e.g., *Lobophyllia* and *Porites*) appear to be more tolerant, with lower incidence of bleaching and mortality (Fisk and Done, 1985; Glynn, 1993; Loya et al., 2001; Baird and Marshall, 2002; Pratchett et al., 2013; Hughes et al., 2017; Harrison et al., 2018; but see Guest et al., 2016). Differences in bleaching responses among taxa have been linked to a variety of traits related to both the coral host (e.g., densities of fluorescent proteins: Salih et al., 2000; mass transfer rates: van Woesik et al., 2012; respiration rates and colony integration: Baird and Marshall, 2002; reviewed in Wooldridge, 2014) and their photosynthetic symbionts (e.g., clade type: Rowan et al., 1997; symbiont plasticity: Grottoli et al., 2014; also see Baker, 2004). Regardless of the mechanism, differential bleaching susceptibility among coral taxa in the Great Barrier Reef Marine Park (GBRMP) has resulted in dramatically altered coral communities (Johns et al., 2014; Hughes et al., 2018b;

Hughes et al., 2019a; Pratchett et al., 2020), with potential long-term consequences for ecosystem function (Richardson et al., 2018; McWilliam et al., 2020). Importantly, the cumulative effects of multiple disturbances will likely incur different community responses (Hughes et al., 2019b; Marzonie et al., 2022), though some taxa (e.g., *Acropora*) appear disproportionately susceptible to a range of disturbances (Pratchett et al., 2014; Hughes et al., 2018b; Madin et al., 2018; Keesing et al., 2019).

Coral colony size has also been suggested to influence bleaching susceptibility and subsequent mortality (Hoeksema, 1991; Mumby, 1999; Loya et al., 2001; Shenkar et al., 2005; Brandt, 2009; van Woesik et al., 2012; Depczynski et al., 2013; Pratchett et al., 2013; Álvarez-Noriega et al., 2018). Small corals have less resources and a smaller surface area and are therefore more likely to suffer whole colony mortality than partial mortality by any given disturbance (Madin et al., 2014). Despite this, some studies suggest small corals may be more resistant to bleaching than larger colonies (Mumby, 1999; Shenkar et al., 2005; Depczynski et al., 2013) due to favourable surface area to volume ratios and/or the diversity of symbionts they harbour. Some coral species harbour a greater variety of symbiont types during early ontogeny, possibly allowing for a more flexible bleaching response than their adult conspecifics (e.g., *Acropora tenuis*: Abrego et al., 2008, 2009). Small colonies also have significantly higher mass transfer rates than larger colonies owing to their high surface area to volume ratio, allowing for more efficient diffusion of both CO_2 and oxygen radicals and subsequent maintenance of photosynthesis (van Woesik et al., 2012). But even within taxa, size-based bleaching response appears to vary among locations and bleaching events. For example, small (<5 cm diameter) *Pocillopora* colonies at Lizard Island in the GBRMP were reported to be more susceptible to bleaching mortality than larger congeners (>5 cm diameter) during the 2016 bleaching event (Álvarez-Noriega et al., 2018). However, small *Pocillopora* corals (<10 cm diameter) were found to be less susceptible to bleaching than their larger congeners (>50 cm diameter) during an earlier bleaching event in French Polynesia (Pratchett et al., 2013). Variability in size selectivity within taxonomic groups, among regions could be related to differences in species composition within a genus, symbiont type, genotype or the host's ability to switch or shuffle symbionts (Goulet, 2006; Sampeyo et al., 2008), but the mechanisms behind this inconsistency in size-based bleaching are still unknown. The disproportionate loss of larger corals following concurrent bleaching events would impact stock-recruitment relationships and impair recovery potential of coral assemblages (Hughes et al., 2019a; Pisapia et al., 2020). However, the persistence of juveniles may act as a buffer against shifts in community composition and aid in recovery following such disturbances (Chong-Seng et al., 2014; Álvarez-Noriega et al., 2018; Doropoulos et al., 2021).

Differential bleaching susceptibility (both within and among taxa) may influence the population and community structure of reef-building corals, though the selectivity of such disturbances is inherently linked to the magnitude of marine heatwaves and corresponding severity of mass-bleaching episodes (Hughes et al., 2017, 2018b). The greatest selective pressures on coral community composition and size structure are likely realised under moderate heatwaves and bleaching episodes as only the most sensitive corals will be affected. In contrast, extreme heatwaves will likely result in high incidence of bleaching and mortality across all corals, regardless of size or species (Hughes et al., 2017). It is often assumed therefore, that increasingly severe mass-bleaching events simply affect an ever-increasing range of different coral taxa, and the most susceptible species are always the first and worst affected (Hughes et al., 2017).

The objective of this study was to explicitly test for differences in bleaching susceptibility among major coral taxa and colony size classes relative to the overall proportion of corals that bleached in 2020 at each of 33 reefs (reef-scale bleaching severity) across Australia's Great Barrier Reef Marine Park (GBRMP) and Coral Sea Marine Park (CSMP). With accelerating climate change, and unprecedented disturbances on coral reefs, we are having to re-assess much of what we know about the vulnerability and resilience of coral assemblages (Hughes et al., 2018b; Hughes et al., 2019b; McWilliam et al., 2020). Previous coral bleaching events, combined with a suite of other acute and chronic disturbances, have already altered both size structure and taxonomic composition of coral assemblages (Johns et al., 2014; Hughes et al., 2018b; Mellin et al., 2019; Dietzel et al., 2020). Many of the bleaching susceptible taxa (e.g., *Acropora*) are already much less common on reefs subject to recurrent disturbances (e.g., Pratchett et al., 2011) and there is evidence to suggest coral colonies are getting smaller (Pisapia et al., 2020; Dietzel et al., 2020). Contemporary knowledge of colony size and taxon-based susceptibility to coral bleaching is, therefore, critical to inform potential effects of sustained and ongoing ocean warming on the structure and function of coral reef ecosystems.

2. Methods

2.1. Survey sites

This study is based on field surveys conducted from 16 February to 23 March 2020, during a widespread mass-bleaching event in the Great Barrier Reef Marine Park (GBRMP) and adjacent Coral Sea Marine Park (CSMP). Heat stress was spatially extensive and severe across this region, with many reefs exceeding levels of heat stress expected to elicit coral bleaching (Supp fig. 1). Sampling was conducted at 17 reefs on the GBRMP and 16 reefs in the CSMP (Fig. 1). At each reef 1–6 sites (n = 90 sites) were surveyed. Sites were generally positioned on the outer rim (i.e., avoiding lagoon habitat) of reefs where there was continuous reef matrix with well-defined shallow crest (~2 m depth) and adjacent slope extending into deeper water, to ensure comparable habitats were sampled across reefs.

2.2. Bleaching susceptibility

To quantify size- and taxon-based bleaching susceptibility, three replicate 10 × 1 m belt transects were surveyed in each of two habitats, the reef slope (~8–10 m depth) and the reef crest (~2 m depth), at each site. Each transect was laid parallel to the reef contour and at a constant depth, with 40-50 m between adjacent transects. All scleractinian corals within each belt were identified to genus, and further resolved (where appropriate) into morphological groups (e.g., acroporids were split into 'tabular', 'staghorn' and 'other' and poritids into 'massive', 'branching', and 'encrusting with uprights' (e.g., *Porites rus*)). The 10 most common morpho-taxa (hereafter referred to as 'taxa') were selected for our statistical model, where only taxa with >5 colonies present in each bleaching category and size class were included in the model. The taxa 'other *Acropora*' and 'massive *Porites*' were selected in our model and are henceforward referred to throughout as '*Acropora*' and 'massive *Porites*', respectively. Each coral was placed into one of five size classes based on maximum colony diameter (juveniles: ≤5 cm, small: 6-20 cm, medium: 21-40 cm, large: 41-60 cm and very large: >60 cm diameter) and later collapsed into two classes (juveniles: ≤5 cm and adults: >5 cm diameter) to increase power in the model. For all colonies ≤5 cm maximum diameter, a concerted effort was made to discern sexually derived juveniles from small colonies resulting from fission of larger colonies. It should be noted, however, that some small colonies classified here as 'juveniles' may include ramets derived from the partial mortality of larger colonies. Bleaching status of individual colonies was scored based on eight health categories (Healthy; Pale; <50 % partially bleached; >50 % partially bleached; 100 % bleached; 5–50 % bleaching-induced partial mortality; 51–99 % bleaching-induced partial mortality; and 100 % bleaching-induced recent mortality). These health categories were later pooled binomially as either 'bleached' (inclusive of pale colonies through to bleaching-induced recent mortality) or 'not bleached' to allow for greater statistical power.
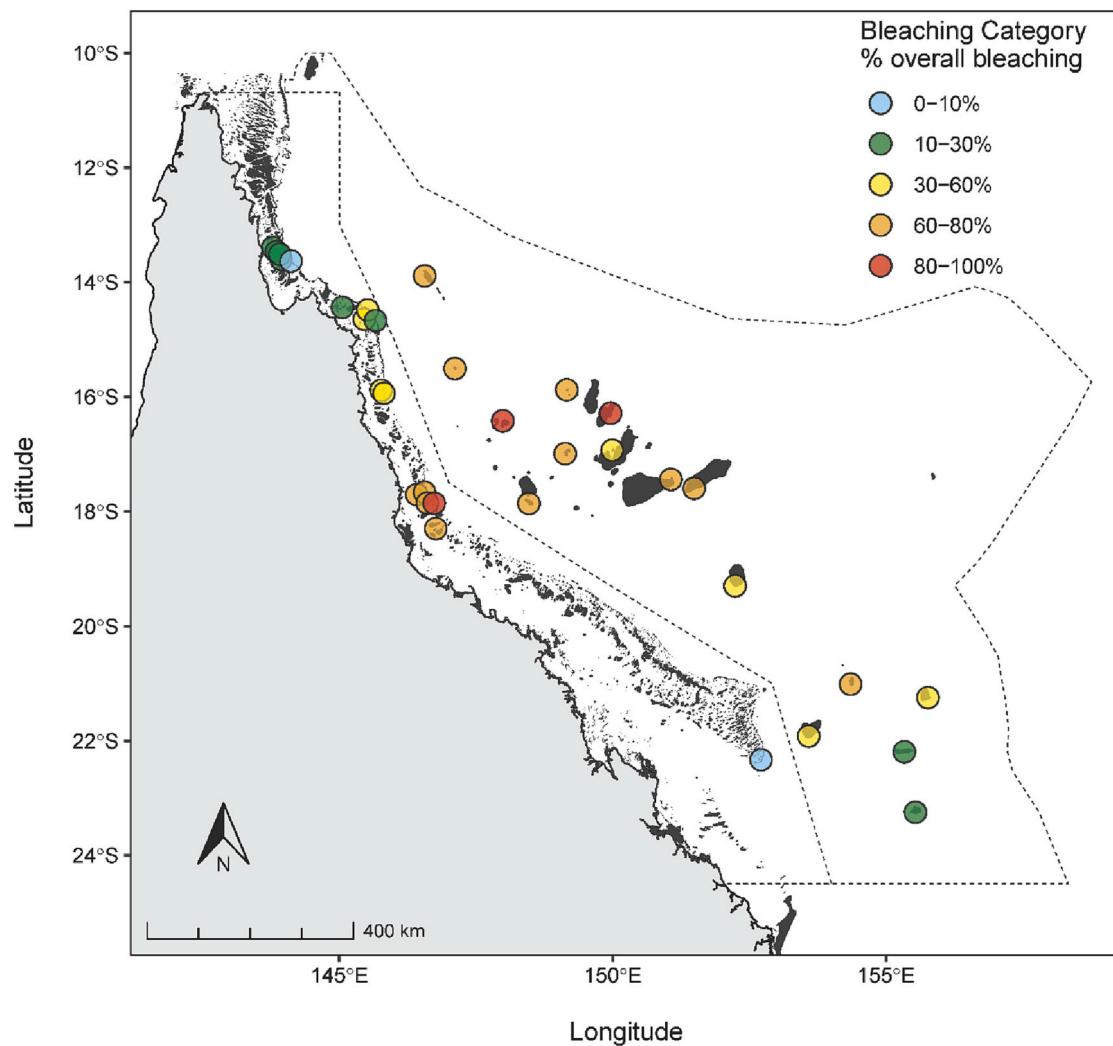
Fig. 1. Map of 33 reefs surveyed in the Coral Sea Marine Park and Great Barrier Reef Marine Park in February–March 2020. Colours represent the reef-scale bleaching severity category for each reef, determined by the overall percent of corals surveyed on each reef that were bleached. Dotted lines represent marine park boundaries, with the Great Barrier Reef Marine Park adjacent to the coast, and the Coral Sea Marine Park directly to the East.

2.3. Statistical analyses

There is increasing evidence that temperature measurements (e.g., Degree Heating Weeks, DHW) alone are not reliable indicators of bleaching severity, especially following concurrent disturbances (DeCarlo and Harrison, 2019; McClanahan et al., 2019; McClanahan et al., 2020). Rather, a suite of interacting factors (e.g., sunlight, water flow, nutrient levels, historic temperature variability, rate of temperature increase) have been shown to affect the susceptibility of corals to bleaching (Maina et al., 2008; Grottoli et al., 2014; Ainsworth et al., 2016; Safaie et al., 2018; Sully et al., 2019; DeCarlo et al., 2020; Winston et al., 2022; Sahin et al., 2023). Therefore, rather than use one or more metrics of heat stress, we used a proxy for reef-scale bleaching severity that is independent of the likely causes of bleaching and simplified the modelling framework. Each of the 33 reefs were assigned to one of five levels of reef-scale bleaching severity based on the overall proportion of colonies that were bleached across all sites and habitats surveyed; i) 'low' (0–10 % bleaching), ii) 'moderate' (11–30 % bleaching), iii) 'high' (31–60 % bleaching), iv) 'very high' (61–80 % bleaching) and v) 'extreme' (>80 % bleaching), following Hughes et al. (2017). The levels of reef-scale bleaching severity assigned also related to the severity of bleaching recorded at the colony scale. The proportion of colonies experiencing 100 % bleaching (i.e., total loss of zooxanthellae) and/or partial mortality resulting from bleaching (as opposed to partial bleaching or paling) increased with each increasing reef-scale bleaching severity category (Supp fig. 2). The taxonomic composition of coral communities did not differ among severity categories (PERMANOVA: F = 1.11, df = 2, R^2 = 0.137, p = 0.339). Corals were more likely to bleach on the reef crest compared to the reef slope, which was consistent among genera and reef-scale bleaching severity categories (see supplementary material for statistical model; Supp fig. 3). Therefore, data were pooled across habitats in the final analysis.

A Bayesian hierarchical generalized linear model was constructed to investigate the effects of three variables (reef-scale bleaching severity, taxa, and colony size) on bleaching susceptibility. Three two-way interactions between taxa, reef-scale bleaching severity, and colony size were modelled to investigate how bleaching susceptibility among taxa varied with respect to both colony size and reef-scale bleaching severity. Additionally, region (GBRMP vs CSMP) was included as a random factor to account for different bleaching susceptibilities between oceanic and continental shelf reefs. The model was fit against a zero-one inflated beta distribution, using weakly informative priors. Posteriors were generated via a No-U-Turn sampler (NUTS), run for 5000 iterations (excluding the first 1000 warmup samples) from each of the three chains, with a thinning rate of 10. All chains were found to be well mixed and converged (Rhat ~1) on a stable posterior. Goodness of fit was assessed

statistically using leave-one-out cross-validation, ensuring all Pareto-k estimates were below 0.5, and visually using a posterior probability check.

Marginal effects plots with 66 % and 90 % highest posterior density credible intervals (CrI) and posterior distributions were produced to show how bleaching susceptibility varied with respect to taxa, reef-scale bleaching severity and colony size individually as well as marginal effects plots to show the interactive effects. CrI reported in the text refer to 90 % CrI. Pairwise contrasts are reported as odds ratios, meaning that where the upper and lower bounds of the associated CrI contain 1, very strong evidence of a difference is not found.

All data was analysed using R 4.1.1 (R Core Team, 2021) using the "brms" package to fit the hierarchical models (Bürkner, 2017), with the "emmeans" (Lenth, 2019) package used for pairwise comparisons of marginal means, and computation of 66 % and 90 % CrI. Comparisons of coral composition among bleaching severity categories were conducted using the "vegan" (Oksanen et al., 2020) package.

3. Results

Of the 38,414 distinct coral colonies within the 10 most common taxa recorded across the 90 sites, 22,129 (57.6 %) colonies displayed some signs of bleaching, ranging from apparent paling or localised and partial bleaching to extensive bleaching or recent mortality of the entire colony. The factors affecting the likelihood of a colony to bleach are complex, as evidenced by three positive two-way interactions in our model. Whilst some taxa (e.g., *Stylophora:* 64 % [CrI 49–85 %]; *Pocillopora:* 54 % [CrI 37–76 %]; and *Goniastrea:* 54 % [CrI 34–73 %]) had a higher tendency to bleach than others (Supp fig. 4a), the likelihood of

different taxa to bleach was dependent on colony size, and on reef-scale bleaching severity (Fig. 2a, b). Furthermore, whilst juvenile corals (≤5 cm diameter) were generally less likely to bleach than adult corals (>5 cm diameter) (juveniles: 44 % [CrI 25–65 %]; adults: 48 % [CrI 29–68 %]; contrast ratio: 1.16 [CrI 1.01–1.32]; Supp fig. 4b, Supp table 1a), this was contingent on the coral taxon, and the severity of the bleaching (Fig. 3).

The rank order of bleaching susceptibility among taxa was dependent on the reef-scale bleaching severity, shown clearly by the interaction between taxa and bleaching severity in our model (Fig. 2a). When reef-scale bleaching severity was low (0–10 %) or extreme (81–100 %), posterior distributions for the likelihood of bleaching among taxa converged, and differential susceptibility among taxa was not clear. However, moderate (11–30 %) to high (31–60 %) severity categories produced the most pronounced differential susceptibilities among the 10 modelled taxa (Fig. 2a). Under conditions of moderate (11–30 %) reef-scale bleaching severity, there was strong evidence that the likelihood of bleaching in *Stylophora* (45 % [CrI 26–68 %]) and *Pocillopora* (43 % [CrI 23–63 %]) was higher than all but one of the other taxa in the model (Fig. 2a; Supp table 2). Under conditions of high (31–60 %) reef-scale bleaching severity, *Stylophora* (73 % [CrI 56–89 %]) and *Pocillopora* (66 % [CrI 49–85 %]) remained very likely to bleach more than all other taxa modelled, but the likelihood of bleaching increased for several other taxa (*Montipora*: 55 % [CrI 34–75 %], *Astrea*: 55 % [CrI 33–75 %], *Goniastrea*: 54 % [CrI 31–73 %], and *Acropora* 53 % [CrI 34–74 %]; Fig. 2a; Supp table 2). Notably, during low to high (0–10 % - 31-60 %) reef-scale bleaching severities, massive *Porites* was consistently among the least likely taxa to exhibit bleaching (Low: 16 % [CrI 4–31 %]; Moderate: 20 % [CrI 7–34 %]; High: 30 % [CrI 12–46 %]; Fig. 2a; Supp
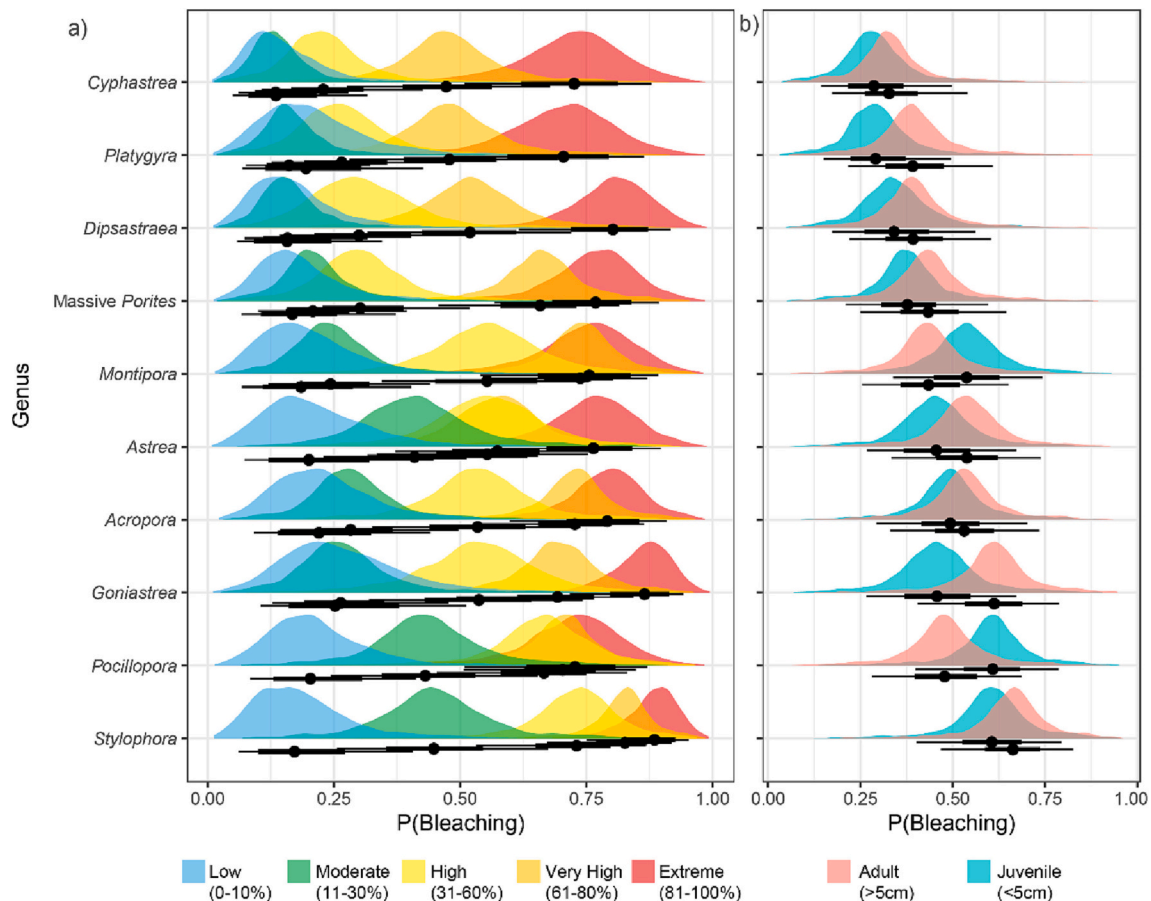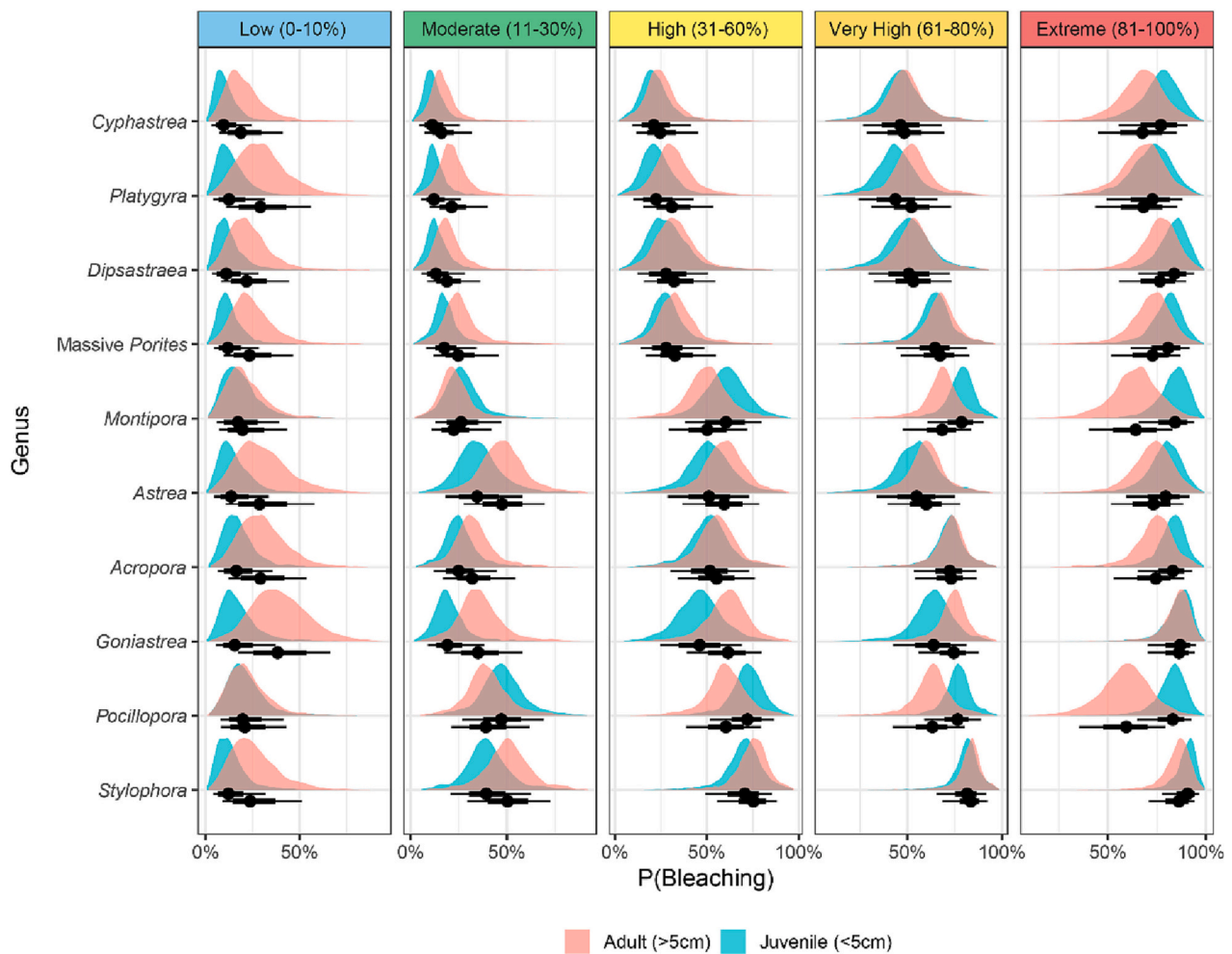

Fig. 2. Marginal posterior distributions for the interactions between taxa and reef-level bleaching severity (a) and taxa and colony size (b). Points represent estimated marginal means, thick and thin lines represent 66 % and 90 % credible intervals, respectively.

Fig. 3. Marginal posterior distributions for the interaction between taxa and size class, varying by reef-level bleaching severity. Each panel represents a reef-scale bleaching severity category, with blue distributions representing juvenile colonies and red distributions representing adult colonies per taxon. Points represent estimated marginal means, thick and thin lines represent 66 % and 90 % credible intervals, respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

table 2), but during very high (61–80 %) reef-scale bleaching severities, massive *Porites* appeared among the most susceptible taxa (66 % [CrI 47–82 %]), becoming much more likely to bleach in comparison with *Cyphastrea* (contrast ratio: 0.46 [CrI 0.31–0.66]), *Dipsastraea* (contrast ratio: 0.56 [CrI 0.35–0.80]) and *Platygyra* (contrast ratio: 0.48 [CrI 0.30–0.67]) colonies (Fig. 2a; Supp table 2). In fact, the rank order of taxonomic bleaching susceptibility shifted considerably depending on the reef-scale bleaching severity category (Fig. 2a).

The rank order of taxonomic susceptibility was also somewhat dependent upon the colony size (Fig. 2b). For five of the ten taxa modelled (*Astrea, Goniastrea, Platygyra,* massive *Porites* and *Stylophora*), there was evidence that adult corals were more likely to bleach than their juvenile congeners, with strong evidence that *Goniastrea* and *Platygyra* adults bleach more readily than the juveniles (*Goniastrea* adults: 61 % [CrI 46–83 %]; *Goniastrea* juveniles: 46 % [CrI 26–67 %]; *Goniastrea* contrast ratio: 1.87 [CrI 1.18–2.62]; *Platygyra* adults: 39 % [CrI 19–57 %]; *Platygyra* juveniles: 29 % [CrI 11–45 %]; *Platygyra* contrast ratio: 1.59 [CrI 1.01–2.24]; Fig. 2b; Supp table 1b). However, the opposite was found for *Pocillopora* and *Montipora*, where the likelihood of bleaching in juveniles was very high when compared to congeneric adults (*Pocillopora* adults: 48 % [CrI 28–67 %]; *Pocillopora* juveniles: 61 % [CrI 44–81 %]; *Pocillopora* contrast ratio: 0.59 [CrI 0.41–0.79]; *Montipora* adults: 43 % [CrI 27–66 %]; *Montipora* juveniles: 54 % [CrI 33–74 %]; *Montipora* contrast ratio: 0.66 [CrI 0.44–0.92]). For three taxa (*Acropora, Cyphastrea* and *Dipsastraea*), there was no evidence

of a difference in the bleaching susceptibility between colony sizes (Fig. 2b; Supp table 1b). Assessing different colony sizes resulted in a different rank order of taxonomic susceptibility to coral bleaching, but this is likely to also be contingent upon the severity of the bleaching.

The differential susceptibility to bleaching between the two size classes was most pronounced during low (0–10 %), moderate (11–30 %) and extreme (81–100 %) reef-scale bleaching severities. Adult corals were much more likely to bleach at lower severities compared with juvenile corals (adults (low): 25 % [CrI 11–43 %]; juveniles (low): 13 % [CrI 4–24 %]; contrast ratio (low): 2.11 [CrI 1.25–3.04], and much less likely to bleach than juveniles at extreme severities (adults (extreme): 74 % [CrI 59–90 %]; juveniles (extreme): 83 % [CrI 71–94 %]; contrast ratio (extreme): 0.59 [CrI 0.42–0.78]; Fig. 3, Supp table 3).

Estimates were also computed for the interactions between taxa and colony size for each reef-scale bleaching severity category (Fig. 3). The differential susceptibility between size classes changed for some taxa depending on the reef-scale bleaching severity (Fig. 3). Most taxa followed the results of the two-way interactions, where juveniles were less likely to bleach at lower severities and more likely to bleach at extreme severities. For example, juvenile *Acropora* colonies were much less likely to bleach than their adult counterparts during low (0–10 %) reef-scale bleaching severity (*Acropora* adult (low): 29 % [CrI 10–50 %]; *Acropora* juvenile (low): 16 % [CrI 4–31 %]; *Acropora* contrast ratio (low): 2.12 [CrI 1.12–3.26]). In contrast, juvenile *Acropora* colonies were equally likely to bleach as the adults during moderate, high and very

high severities, and became much more likely to bleach during extreme (81–100 %) severities (*Acropora* adult (extreme): 74 % [CrI 59–93 %]; *Acropora* juvenile (extreme): 83 % [CrI 69–95 %]; *Acropora* contrast ratio (extreme): 0.59 [CrI 0.35–0.83]). However, juvenile *Pocillopora* and *Montipora* were unlikely to show increased bleaching likelihood in comparison to their adult congenerics at low reef-scale bleaching severities (*Pocillopora* adults (low): 21 % [CrI 6–38 %]; *Pocillopora* juveniles (low): 20 % [CrI 5–35 %]; *Pocillopora* contrast ratio (low): 1.07 [CrI 0.57–1.67]) and became much more likely to bleach than their adult congenerics as severity increased (Fig. 3; Supp Table 4). For some taxa, such as *Goniastrea* and *Platygyra*, the juveniles remained much less likely to bleach than adult congenerics, until bleaching severity became extreme (81–100 %), whereby the likelihood of adults bleaching was equal to that of juveniles (Fig. 3; Supp table 4).

4. Discussion

The incidence of mass bleaching recorded during 2020 in the Great Barrier Reef Marine Park (GBRMP) and the Coral Sea Marine Park (CSMP) varied greatly among coral taxa, reflecting widely reported taxonomic differences in bleaching susceptibility (e.g., Brown and Suharsono, 1990; Glynn, 1993; Loya et al., 2001; Baird and Marshall, 2002; Guest et al., 2012; Bayraktarov et al., 2013; Pratchett et al., 2013; Hughes et al., 2018b; Pisapia et al., 2019). However, taxonomic differences in bleaching susceptibility did not simply become less apparent with increases in reef-scale bleaching severity. Rather, the rank order of the bleaching susceptibility was dependent on our proxy of bleaching severity (see also Hughes et al., 2017) with different coral taxa being disproportionately affected during low versus high levels of reef-scale bleaching severity. For example, massive *Porites* exhibited very low incidence of bleaching on reefs where reef-scale bleaching severity was low to high (i.e., <60 % of colonies bleached), but was among the most susceptible taxa at reefs with very high (61–80 % of colonies bleached) and extreme (>80 % of colonies bleached) bleaching severity (Fig. 2a). Massive *Porites* are generally considered to be among the least susceptible coral taxa to temperature stress (Loya et al., 2001; Hughes et al., 2017), though massive *Porites* do bleach and sometimes die during particularly severe heatwaves, when bleaching impacts even the most thermally tolerant corals, or during recurrent bleaching events (Grottoli et al., 2014; Burn et al., 2022). Our data suggest that massive *Porites* are disproportionately affected during severe bleaching, such that increasingly severe bleaching events may ultimately lead to declines in abundance of these corals. Any declines in the abundance of massive *Porites* will be further compounded by their slow growth and limited capacity for recovery in the aftermath of such disturbances (Pratchett et al., 2020; Morais et al., 2021).

While bleaching susceptibility varied with reef-scale bleaching severity for some coral taxa (most notably, massive *Porites*), there were also some taxa that were more or less impacted than others regardless of overall bleaching severity. Therefore, despite more severe events being likely to affect a wider range of coral taxa than mild events, it appears a subset of sensitive taxa will always be disproportionately more affected than others. The susceptibility of these taxa is consistent with those of other studies where fast growing, branching taxa (e.g., *Stylophora*, *Pocillopora* and *Acropora*) were more likely to bleach than slow growing, massive taxa (Fisk and Done, 1985; Brown and Suharsono, 1990; Glynn, 1993; Fujioka, 1999; Marshall and Baird, 2000; Loya et al., 2001; Baird and Marshall, 2002; Pratchett et al., 2013; Harrison et al., 2018; Hughes et al., 2018b). However, there were some notable exceptions. *Goniastrea* was among the most susceptible in our study, similar to findings from Thailand and the GBRMP (Brown et al., 2014; Hughes et al., 2017). In contrast, Loya et al. (2001) reported minimal change in the cover and abundance of *Goniastrea* following the 1998 bleaching in Japan, leading to suggestions it was one of the more bleaching tolerant coral taxa. It may be that *Goniastrea* is highly susceptible to bleaching but rarely dies, and it is rates of whole colony mortality that ultimately dictate

differential susceptibility to mass-bleaching and corresponding shifts in coral assemblages (van Woesik et al., 2011). Alternatively, differences in the species composition of *Goniastrea* among locations (including recent changes in the taxonomy of *Goniastrea*; Huang et al., 2014) may have contributed to the differences among studies. Similarly, differences in the composition of coral species, symbionts, or genotypes within coral genera may have contributed to the observed differences in bleaching susceptibility in our study (Manzello et al., 2018; Marzonie et al., 2022).

With the most sensitive taxa bleaching at lower reef-scale severities, changes in composition are likely to occur following low to mid-level bleaching incidence, especially given the predisposition of those corals to be the primary target of other major disturbances occurring on the reef (i.e., crown-of-thorns starfish: Keesing et al., 2019; severe storms: Madin et al., 2018). Changes in community composition are however, dependent on incidence of bleaching translating to colony mortality, which for lower severity bleaching may take several months to manifest (Baird and Marshall, 2002), if at all. However, as the severity of the temperature stress increases, and a wider subset of coral taxa are affected by bleaching, future community composition is likely to be shaped by the differential mortality and/or recovery of coral taxa, rather than differential bleaching susceptibility (Leggat et al., 2019; Pratchett et al., 2020). Moreover, the large distances (typically >100 km) and deep waters (1-3 km deep) separating reefs within the CSMP, and CSMP reefs from adjacent reef systems (e.g., GBR and New Caledonia), may limit the larval input from other reefs (Ceccarelli et al., 2013). This could constrain replenishment of coral populations and exacerbate shifts in the composition of coral communities, especially if disturbances are frequent and severe (Gilmour et al., 2013). Further monitoring of these populations may provide important insights into possible shifts in community structure.

Whilst some studies have provided evidence of increasing bleaching tolerance in susceptible taxa (e.g., *Acropora*) following recurrent bleaching events (Guest et al., 2012; Pratchett et al., 2013), we found the differential susceptibilities of those thermally sensitive taxa are much the same as those reported in past studies from the GBRMP and CSMP (Marshall and Baird, 2000; Hughes et al., 2017; Harrison et al., 2018). Further work should be conducted to determine if any temporal changes exist in taxonomic bleaching susceptibility in the CSMP and GBRMP following this most recent event. This is particularly important, especially considering the effects of past disturbances are likely to influence effects of those in the future (Hughes et al., 2019b) and as the effects of potential protective mechanisms diminish with climate change (Ainsworth et al., 2016).

Overall, juvenile corals (≤5 cm diameter) exhibited lower incidence of bleaching (44 %) than adult (>5 cm diameter) colonies (48 %). Lower bleaching susceptibility in juvenile corals has been documented previously (Hoeksema, 1991; Mumby, 1999; Loya et al., 2001; Brandt, 2009; Phongsuwan and Chansang, 2012; Depczynski et al., 2013) and is generally attributed to symbiont type or mass transfer efficiency (reviewed in Wooldridge, 2014). However, some existing studies do report contrasting patterns of size-based differences in bleaching susceptibility (Álvarez-Noriega et al., 2018; Loya et al., 2001; Brandt, 2009) and we similarly show herein, that the bleaching response is taxon-specific, and dependent on the severity of the bleaching. Transformations in coral size structure and topographic complexity may therefore be exacerbated by susceptibility of specific colony size classes or influenced by the severity of the bleaching event. There is some suggestion that community size structure is shifting toward dominance of smaller coral colonies, owing to the increased turnover following recurrent disturbances (Done, 1999; Pisapia et al., 2020, but see Dietzel et al., 2020). This could benefit taxa whose juveniles were most tolerant to bleaching (e.g., *Stylophora*, massive *Porites*, *Platygyra*, and *Astrea*) and those that mature at smaller colony sizes, but negatively impact taxa whose juveniles were significantly more susceptible (e.g., *Montipora* and *Pocillopora*).

In conclusion, this study shows that taxonomic differences in

bleaching susceptibility are contingent upon both overall bleaching severity and colony size. Differing severities among locations and events will therefore, be likely to result in different community compositions, with moderate stress events highlighting taxonomic differences in the susceptibility to bleaching more clearly than extreme events, where almost all zooxanthellate corals are likely to be susceptible to bleaching. Furthermore, our study highlights the need to account for the size structure of a coral assemblage when determining bleaching susceptibility, where differential susceptibility of certain colony sizes may lead to shifts in size structure for some taxa. As bleaching events become more frequent, it is likely that coral genera with high tolerance for heat stress, such as *Cyphastrea, Platygyra* and *Dispastraea* will be selected for (Álvarez-Noriega et al., 2018; Hughes et al., 2019a), but if bleaching events become more severe, it is likely that the abundance of even these heat-tolerant taxa will significantly decrease. To further understand what future assemblages on corals reefs may look like, we need to continuously monitor both community size structure and composition following disturbances of differing severities. Understanding the initial susceptibility combined with the long-term effects of disturbance and other demographic traits influencing the capacity to recover will be paramount in elucidating the long-term effects of bleaching events on coral communities. Future research should aim to understand what proportion of bleached corals recover so we may better understand the relationship between bleaching susceptibilities and likelihood of bleaching related mortality. Finally, as this 2020 event was the third major bleaching event in five years on reefs in the GBRMP and CSMP, it is important to examine the temporal implications of recurrent bleaching effects on coral assemblages. Combined, this knowledge will give us a much clearer understanding of how coral assemblages will persist into the future.

CRediT authorship contribution statement

D. Burn: Conceptualization, Methodology, Validation, Investigation, Data curation, Writing – original draft. **A.S. Hoey:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition. **S. Matthews:** Methodology, Formal analysis, Resources, Data curation, Writing – review & editing, Visualization. **H.B. Harrison:** Conceptualization, Writing – review & editing, Funding acquisition. **M.S. Pratchett:** Conceptualization, Methodology, Resources, Writing – review & editing, Supervision, Funding acquisition.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.marpolbul.2023.114907.

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