



**HAL**  
open science

## Hot spots of bleaching in massive *Porites* coral colonies

Juliano Morais, Sterling B Tebbett, Renato A Morais, David R Bellwood

► **To cite this version:**

Juliano Morais, Sterling B Tebbett, Renato A Morais, David R Bellwood. Hot spots of bleaching in massive *Porites* coral colonies. *Marine Environmental Research*, 2024, 193, pp.106276. 10.1016/j.marenvres.2023.106276 . hal-04653048

**HAL Id: hal-04653048**

**<https://univ-perp.hal.science/hal-04653048v1>**

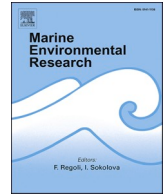
Submitted on 18 Jul 2024

**HAL** is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.



Distributed under a Creative Commons Attribution 4.0 International License



## Hot spots of bleaching in massive *Porites* coral colonies

Juliano Morais<sup>a,\*</sup>, Sterling B. Tebbett<sup>a</sup>, Renato A. Morais<sup>a,b</sup>, David R. Bellwood<sup>a</sup>

<sup>a</sup> Research Hub for Coral Reef Ecosystem Functions, College of Science and Engineering, James Cook University, Townsville, Queensland, 4811, Australia

<sup>b</sup> Paris Sciences et Lettres Université, École Pratique des Hautes Études, EPHE-UPVD-CNRS, USR 3278 CRIOBE, University of Perpignan, 66860, Perpignan, France

### ARTICLE INFO

#### Keywords:

Coral reef  
Massive *Porites*  
Coral bleaching  
Great barrier reef  
Spatial variation

### ABSTRACT

Coral bleaching events have become more frequent and severe due to ocean warming. While the large-scale impacts of bleaching events are well-known, there is growing recognition of the importance of small-scale spatial variation in bleaching and survival probability of individual coral colonies. By quantifying bleaching in 108 massive *Porites* colonies spread across Lizard Island, Great Barrier Reef, during the 2016 bleaching event, we investigated how hydrodynamic exposure levels and colony size contribute to local variability in bleaching prevalence and extent. Our results revealed that exposed locations were the least impacted by bleaching, while lagoonal areas exhibited the highest prevalence of bleaching and colony-level bleaching extents. Such patterns of bleaching could be due to prolonged exposure to warm water in the lagoon. These findings highlight the importance of considering location-specific factors when assessing coral health and emphasize the vulnerability of corals in lagoonal habitats to rapid and/or prolonged elevated temperatures.

### 1. Introduction

Severe marine heatwaves have intensified coral bleaching events in recent years, leading to high coral mortality rates (Lough et al., 2018; Sully et al., 2019). While there is some evidence of localized natural recovery after these disturbances (Holbrook et al., 2018; Morais et al., 2023), a shortening in the recovery window has led to ongoing regional-scale impacts on coral populations (Vercelloni et al., 2020; Hughes et al., 2021). Large spatial scale (hundreds to thousands of square kilometres) bleaching impacts on coral reefs are now well documented (e.g. Sully et al., 2019; Dietzel et al., 2021). However, the effects of bleaching events can also vary at small spatial scales, spanning from just tens to hundreds of meters (Green et al., 2019; Grimaldi et al., 2023). For individual coral colonies, small-scale spatial variation in exposure to heatwaves may mean the difference between life and death.

At small spatial scales there are various factors that may shape the extent of coral bleaching. For example, variation in reef morphology can interact with water flow, causing some reef areas to heat more than others (Lenihan et al., 2008; Green et al., 2019; Grimaldi et al., 2023). These hydrodynamic process can either exacerbate (DeCarlo et al., 2017) or mitigate (Schmidt et al., 2016) thermal stress from heatwaves. Furthermore, there is evidence to suggest that colony size has an impact on the susceptibility of corals to bleaching (Hughes and Jackson 1985; Shenkar et al., 2005; Wagner et al., 2010; Pratchett et al., 2013). Finally,

the specific coral taxa present at a location may also influence bleaching rates as some corals, such as massive *Porites*, are known to be relatively bleaching resistant (Harrison et al., 2019; Pratchett et al., 2020; Morais et al., 2021), while others, such as *Acropora*, tend to be highly susceptible to bleaching (Van Woesik et al., 2012b; Burn et al., 2023). Given the high mortality rates of susceptible corals (Loya et al., 2001; Pisapia et al., 2019), it has been suggested that in some circumstances corals that are more thermally tolerant, such as massive *Porites*, may become the dominant coral taxa (Pisapia et al., 2019; McClanahan et al., 2020; Pratchett et al., 2020). Although there is a significant body of literature on massive *Porites* bleaching responses across small-spatial scales (<5 km) using artificial bleaching methods (e.g. Barshis et al., 2018; Klepac and Barshis 2020, 2022), our understanding of how this response varies in populations at small scales, across different hydrodynamic exposure levels during natural bleaching events remains limited.

As massive *Porites* may be a key group of corals on some Anthropocene reefs, understanding how bleaching impacts in this genus varies across small spatial scales could be important in helping predict the impacts of heatwaves in the future. To examine this variation, we measured bleaching prevalence (% colonies) and individual extent (% colony area) in 108 massive *Porites* coral colonies during a severe bleaching event in 2016 on Australia's, Great Barrier Reef (GBR). Subsequently, we investigate how hydrodynamic exposure levels and colony size may help explain observed variability in bleaching in *Porites*

\* Corresponding author.

E-mail address: [juliano.morais@my.jcu.edu.au](mailto:juliano.morais@my.jcu.edu.au) (J. Morais).

<https://doi.org/10.1016/j.marenvres.2023.106276>

Received 7 August 2023; Received in revised form 10 November 2023; Accepted 15 November 2023

Available online 19 November 2023

0141-1136/© 2023 The Authors. Published by Elsevier Ltd. This is an open access article under the CC BY license (<http://creativecommons.org/licenses/by/4.0/>).

colonies spread across Lizard Island's 16 km<sup>2</sup> coral reef system.

## 2. Materials and methods

### 2.1. Study area and sampling

Data were collected at Lizard Island (14°40' S, 145°28'E), a mid-shelf island group in the northern region of the GBR. Between February and April 2016, an intense marine heatwave resulted in a severe coral bleaching event in this northern region of the GBR (Hughes et al., 2021). Within this timeframe, the average water temperature at a depth of 0.6 m consistently surpassed 30 °C (see Fig. S3). In April/May 2016, during this bleaching event, and after ~8 Degree Heating Weeks (DHW) (Bainbridge 2017), a series of 19 permanent transects (distances between individual transects ranged from 0.15 to 4.7 km) were surveyed along the reef 'crest' (0–4 m below chart-datum, details in Wismer et al., 2019; Tebbett et al., 2022) (Fig. S2a). Each transect comprised 12–38 quadrats (1 m<sup>2</sup> area). Within transects, each quadrat was placed approximately 5 m apart (with the number of quadrats dependent on reef extent) and photographed (Camera: Nikon Coolpix AW130) from a planar view. All photographs used in the analysis in this study were taken between April 27th and May 5th 2016, which ensures that timing of individual surveys had a minimal effect on bleaching data.

### 2.2. Image processing

From the photographs, we selected all quadrats that included at least one massive *Porites* colony and recorded the number of *Porites* colonies and their bleaching status (i.e. bleached or not bleached). Note that five transects with no quadrats containing at least 1 massive *Porites* colony were excluded from our analysis. To determine the live tissue area, each colony was measured by tracing around visible live coral tissue to obtain the planar area of live tissue in cm<sup>2</sup> (this planar area was considered as the 'colony size'). When a colony was bleached (ranging in colour from pale, i.e. light bleaching, to white, i.e. severe bleaching; all categorized as bleached herein), we also traced around the visibly bleached area, as above. Subsequently, the relative extent of coral bleaching on each colony was calculated based on the planar bleached area as a percentage of the total planar live tissue area. It should be noted that, due to the constraints of our photographic methods, our analysis was limited to the planar area of each colony, which represents a two-dimensional, top-down view of the coral colony surface. Bleaching does not occur uniformly across a coral colony. Typically, areas not exposed to direct sunlight exhibit less bleaching compared to the colony's uppermost parts that receive more sunlight. Therefore, to keep estimates consistent, all photographs were taken from the same perspective, ensuring that we compared equivalent portions of each colony (the planar area). All images were processed using the ImageJ software (Schneider et al., 2012) with the 1 m<sup>2</sup> quadrat serving as a scale.

### 2.3. Statistical analyses

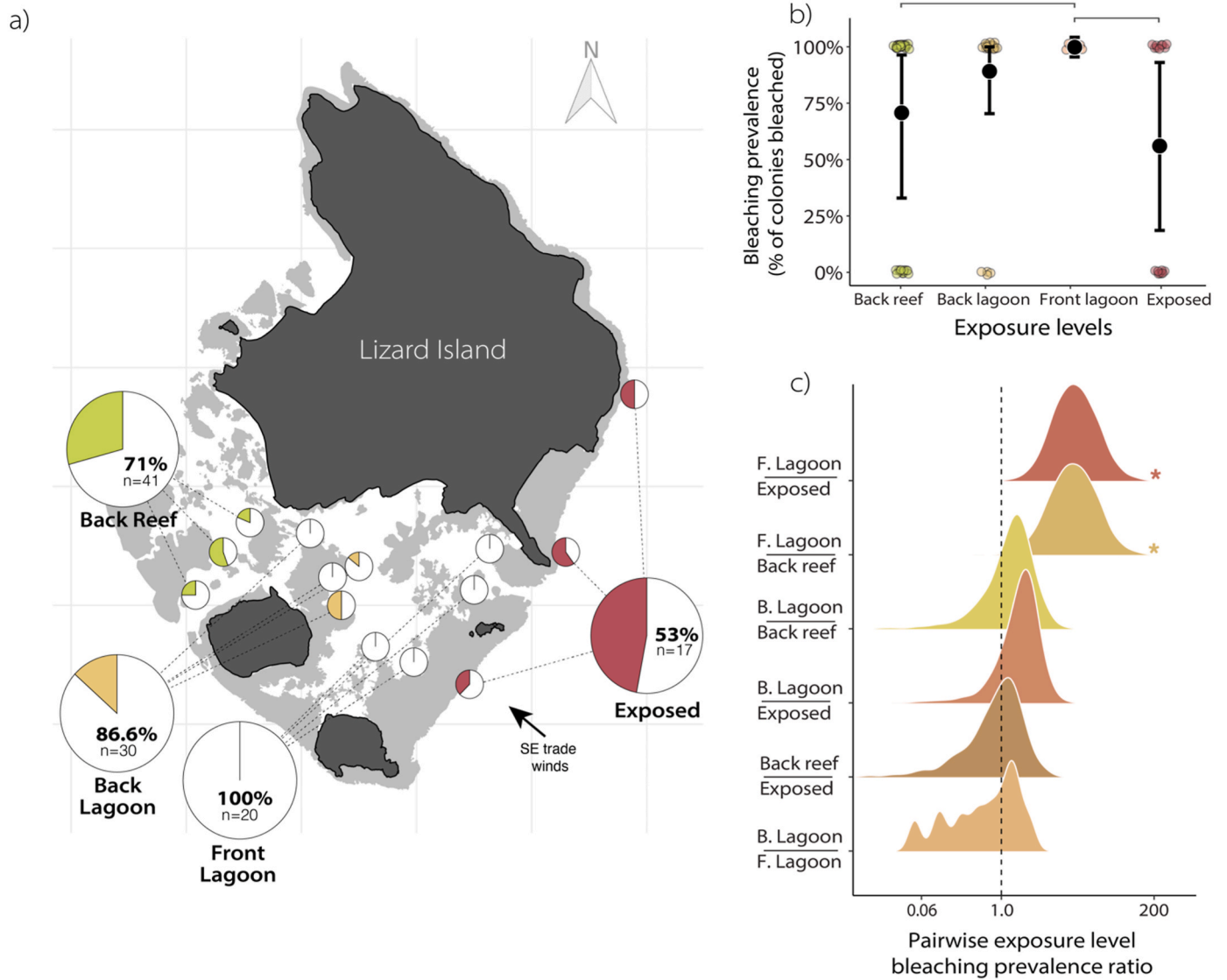
To compare the bleaching prevalence, i.e. the proportion of massive *Porites* colonies that bleached in each exposure level, we used a Bayesian generalized linear mixed effects model with a binomial distribution and logit link. Bleaching status (0 = not bleached, 1 = bleached), was used as the response variable and exposure level (exposed, front lagoon, back lagoon, and back reef), as well as colony size, were treated as interacting fixed effects. The exposure categories were determined based on the transect locations' orientation relative to the prevailing south-east trade winds following (Morais et al., 2022). To investigate the extent of bleaching (% of colony area bleached; the response variable) in bleached massive *Porites* colonies (only colonies with measurable bleaching extent were used in this model [n = 84]), we used a Bayesian generalized linear mixed effects model with a gamma distribution and log link. Again, exposure level and colony size were treated as interacting fixed

effects. In both models, transect identity was also included as a random effect to account for any lack of spatial independence in the sampling design. Each model was based on 3 MCMC chains with 5000 iterations, including 1000 iterations to warm-up and a thinning interval of 3, with weakly informative priors. Model fits and assumptions were assessed using residual and autocorrelation plots, supplemented by metrics of effective sample size (neff) and sampling efficiency (rhat) scores, all of which were satisfactory and showed that the MCMC chains were well mixed and converged. Both Bayesian models were performed in Stan (Stan Development Team, 2021) via the *brms* package (Bürkner, 2017) in the software R (R Core Team, 2020).

## 3. Results and discussion

There were clear differences in the bleaching response of massive *Porites* colonies among exposure levels at Lizard Island during the 2016 bleaching event. Out of the 108 colonies recorded, 84 (77.7%) experienced bleaching to some extent. Exposed locations had the lowest bleaching prevalence with a total of 53% of the colonies bleaching (varying from 40% to 62% among the exposed transects). By contrast, virtually all colonies in the lagoonal habitats were bleached. In the front lagoon, 100% of the colonies experienced bleaching. Meanwhile, in the back lagoon, a total of 86.6% of colonies were bleached, with this percentage varying from 50% to 100% at the transect level. Additionally, there was a high prevalence (total = 71%, ranging from 44% to 75% at the transect level) of colony bleaching on back reefs (Fig. 1a and b). Importantly, our model estimated colonies in the front lagoon to be twice as likely to bleach compared to those in exposed locations and around 1.5 times more likely compared to those in the back reef (Fig. 1c, Table S3). This highlights the spatial variability of bleaching prevalence and the importance of considering location-specific factors when assessing coral responses to disturbance. Indeed, these findings align with earlier studies that also observed a higher prevalence of coral bleaching and/or coral loss following bleaching within lagoonal habitats for a variety of coral groups (Van Woesik et al., 2012a; Green et al., 2019; Tebbett et al., 2022a). However, prior-exposure of coral colonies to higher and more variable temperatures (such as those that occur in coral reef lagoons), have also been found to facilitate thermal acclimatization and adaptation of corals to acute temperature stress (Van Woesik et al., 2012a; Ainsworth et al., 2016; Safaie et al., 2018). While our results align with the first example from previous studies, rather than the latter, both examples highlight the marked spatial variation that can occur across coral reef systems in terms of coral colony bleaching.

Our results of spatial variation in bleaching prevalence were mirrored by patterns of bleaching extent in massive *Porites* colonies. Specifically, of the corals that experienced some bleaching (77.7% of colonies), ~30% of the live tissue area was bleached, on average, although there was again marked spatial variation in this bleaching extent (Fig. 2). As in prevalence, the most severe bleaching impacts, on average ( $\pm$ SD), were recorded in the front and back lagoon locations with  $32.3 \pm 25\%$  (varying from 36% to 64% among back lagoon transects), and  $48.1 \pm 26\%$  (ranging from 21% to 42% among front lagoon transects) of the live tissue area bleached (Fig. 2), while relatively little ( $12.6 \pm 6\%$ , ranging from 9% to 23% at the transect level) of the live tissue area was bleached on colonies in exposed locations. Colonies on back reefs experienced intermediate levels of bleaching ( $26 \pm 12\%$  of live tissue area, ranging from 16% to 32% at the transect level) (Fig. 2). Therefore, the areas that experienced the highest prevalence of bleaching (in terms of percentage of colonies bleached) also experienced the most severe bleaching (in terms of the relative extent of live tissue area bleached). Furthermore, this spatial variation in bleaching extent was supported by our model which revealed strong evidence (i.e. the 95% high posterior intervals did not intersect 0) for differences between all exposure levels (except between the front lagoon versus back reef location, Fig. 2c, Table S5).

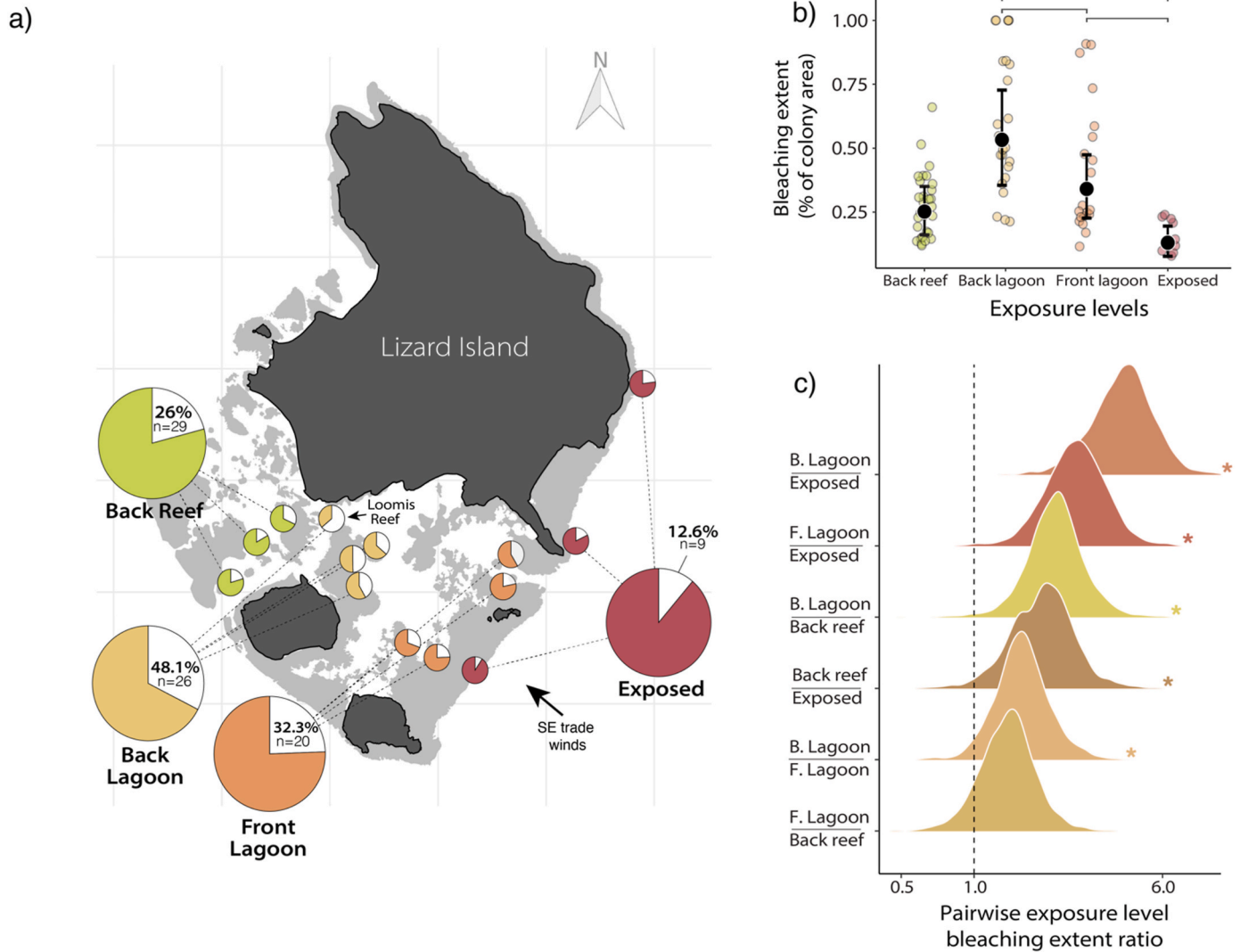


**Fig. 1.** Spatial variation of massive *Porites* bleaching prevalence among exposure levels at Lizard Island, Great Barrier Reef; a) Map showing the bleaching prevalence (i.e., proportion of massive *Porites* colonies with any signs of bleached tissue) on the different transects (small pies) and aggregated by exposure level (large pies). In the pie charts, white segments represent bleached colonies, while colorful segments represent colonies that were not bleached. “n” represents the total number of colonies (bleached + not bleached) sampled in that specific exposure level; b) colony-level bleaching outcomes (coloured dots, 0 = not bleached, 100 = bleached) and the posterior probability of bleaching for massive *Porites* colonies in the different exposure levels. Model fits originated from a binomial Bayesian generalized linear mixed model (with transect as a random effect); c) pairwise comparisons (ratio) of the posterior probability of bleaching for massive *Porites* colonies in the different exposure levels. Distributions with values predominantly exceeding 1 indicate that the exposure level in the numerator had higher probability of bleaching, while distributions with values predominantly lower than 1 indicate that the exposure level in the denominator had higher probability of bleaching. Horizontal bars in ‘b’ and asterisks in ‘c’ represent strong evidence of differences between the categories.

In a previous study, we found that massive *Porites* colonies that experience bleaching on 62% or more of their live tissue area tend to experience substantial levels of partial mortality in the months following the bleaching event (Morais et al., 2021). Of the colonies measured herein, 17% had more than 62% of their live tissue area bleached and almost all of these colonies (98%) were found in lagoonal habitats. Given the spatial distribution of bleaching extent this, therefore, suggests a substantially higher likelihood of tissue loss for massive *Porites* corals in these lagoonal habitats following bleaching.

It is important to recognize that thermal regimes on coral reefs strongly depend on the interaction between water movements and reef morphology (Lenihan et al., 2008; DeCarlo et al., 2017; Grimaldi et al., 2023). Specifically, while exposed sites benefit from strong currents, which can bring cooler water up the fore reef slope (Schmidt et al., 2016;

Storlazzi et al., 2020; Wyatt et al., 2020), lagoonal habitats can experience limited cooler water inputs (Rogers et al., 2016; Grimaldi et al., 2023). Consequently, lagoonal sites can be more prone to rapid local warming, making coral communities there more susceptible to bleaching. However, not all types of water movement on reefs lead to thermal stress reduction. Indeed, at the transect level, the highest average bleaching extent (64%) was located at the sheltered (western) fringe of the main lagoon (Loomis Reef) (Fig. 2a). This particular reef is also exposed to some of the highest average current speeds around Lizard Island (Tebbett et al., 2022b) (Fig. S2). The accelerated water flow, combined with the prevailing current direction, means that Loomis Reef forms a bottleneck for water being discharged from the lagoon (Tebbett et al., 2022b). This water exiting the lagoon is likely to be relatively warm (Green et al., 2019; Grimaldi et al., 2023). Therefore, corals



**Fig. 2.** Spatial variation of massive *Porites* bleaching extent among exposure levels at Lizard Island, Great Barrier Reef; a) Map showing the average bleaching extent (i.e., average percentage of colony live tissue bleached) on the different transects (small pies) and aggregated by exposure level (large pies). In the pie charts, white segments represent % of the live tissue area bleached, while colorful segments represent % of the live tissue area not bleached. “n” represents the total number of bleached colonies in that specific exposure level; b) posterior probability of bleaching extent for massive *Porites* colonies in the different exposure levels. Model fits pertain to a gamma Bayesian generalized linear mixed model (with transect as a random effect), while coloured dots represent individual massive *Porites* colonies (raw data points); c) pairwise comparisons (ratio) of bleached area extent between the different exposure levels (interpretation of Fig. 2c is the same as in Fig. 1c). Horizontal bars in ‘b’ and asterisks in ‘c’ represent strong data evidence of differences between paired categories.

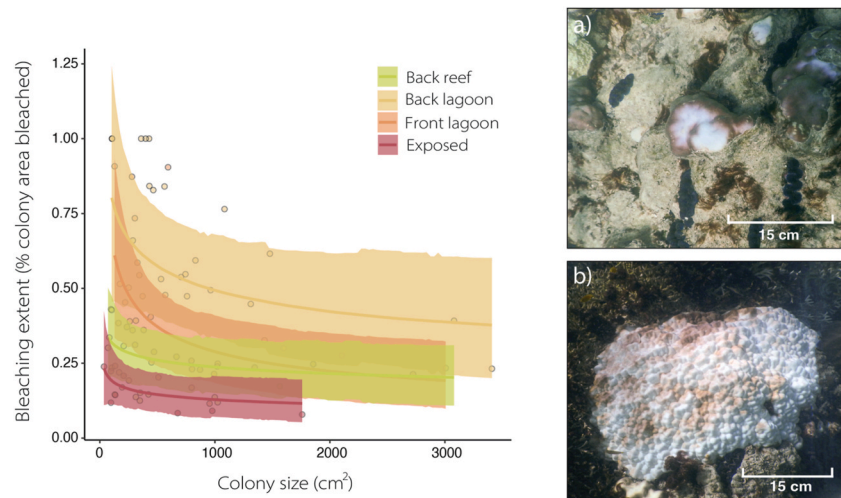
situated in this area likely faced a high flow of heated water, increasing bleaching risk, and presumably explaining the highest *Porites* bleaching prevalence and extent in this area.

Beyond the interaction between reef morphology and hydrodynamics, colony size can also play a role in determining bleaching susceptibility, with an extensive body of literature identifying this relationship for a variety of corals (e.g. Edmunds 2005; Shenkar et al., 2005; Wagner et al., 2010; Pratchett et al., 2013; Burn et al., 2023). However, our models indicated that the size of colonies had no effect on either the prevalence or the extent of bleaching in massive *Porites* (Fig. 3, Fig.S1, Tables S1, S2, S4, S6). The lack of effect found herein may be attributed to the difference in the size range examined in our study compared to other studies. For example, past studies that investigated bleaching using colony size as a variable, explored a relatively small size range of small colonies (e.g. >16 cm<sup>2</sup> to <60 cm<sup>2</sup> [Shenkar et al., 2005]) or compared juvenile colonies (<5 cm diameter) with adults (>5 cm diameter) (e.g. Burn et al., 2023). In contrast, when compared to Burn

et al. (2023), our study focused only on adult colonies (>5 cm diameter), and when compared to Shenkar et al. (2005) our study considered a much larger size range (30.4 cm<sup>2</sup>–3408.8 cm<sup>2</sup>). Indeed, when compared to the size range in Shenkar et al. (2005), only 4.6% of our colonies were smaller than their largest size colony (i.e. <60 cm<sup>2</sup>). To deepen our understanding of the effect of colony size on bleaching susceptibility, future research may also consider the variation in bleaching colour gradient (Chow et al., 2016). A thorough investigation of these aspects could shed even more light on the differential bleaching responses among colonies of varying sizes.

Overall, our study revealed that both the prevalence and extent of bleaching were spatially heterogeneous in massive *Porites* colonies around Lizard Island. Given that both the prevalence and extent of bleaching were highest in the lagoonal habitat, this suggests that corals in this area were either a) more sensitive to thermal stress, or b) exposed to more intense thermal stress during the heatwave. As past evidence has suggested that corals in lagoonal environments tend to be more tolerant





**Fig. 3.** Interaction between colony size and wave exposure level in determining the extent of bleaching on individual massive *Porites* colonies. Note most of the variability is among exposure categories while colony size did not have a large effect on bleaching extent. Model fits were based on a gamma distributed Bayesian generalized linear mixed model (with transect as a random effect). Lines represent model estimated marginal means for different exposure levels. Ribbons denote the 95% high posterior density intervals and points represent bleaching extent of individual massive *Porites* colonies. Photographs showing examples of bleaching in a small (a) and a large (b) massive *Porites* colony at Lizard Island, Great Barrier Reefs. Photographs: RP Streit.

of thermal stress (Ainsworth et al., 2016; Safaie et al., 2018), the latter mechanism may be the primary factor driving spatial variation in bleaching intensity. Restricted water circulation in lagoonal habitats may thus have led to more intense and prolonged exposure to warmer waters (cf. Rogers et al., 2016; Green et al., 2019). Indeed, the highest extent of bleaching was in the location where these lagoonal waters are likely to drain from the lagoon (i.e. Loomis Reef). These findings emphasize the importance of considering location-specific factors, especially reef morphology and hydrodynamics, in assessing coral health and bleaching susceptibility.

#### Author statement

**Juliano Morais:** Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Visualization, Funding acquisition, Writing – original draft. **Sterling B. Tebbett:** Conceptualization, Methodology, Investigation, Visualization, Funding acquisition, Writing – review & editing. **Renato A. Morais:** Conceptualization, Methodology, Investigation, Data curation, Visualization, Writing – review & editing. **David R. Bellwood:** Conceptualization, Methodology, Investigation, Resources, Funding acquisition, Writing – review & editing.

#### Declaration of competing interest

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

#### Data availability

Data will be made available on request.

#### Acknowledgements

We thank R.P. Streit, J.A. Schlaefer, M. Mihalitsis, C. Bowden, C.R. Hemingson, S. Swan, J. Grimm, P. O'Brien, C.H.R. Goatley and the Lizard Island Research Station staff for field support. We also thank the Australian Research Council (DRB: FL190100062), the Ian Potter Foundation (JM, SBT), the Australian Museum's Lizard Island Research Station (JM, SBT), and the International Coral Reef Society (SBT) for financial support.

#### Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.marenvres.2023.106276>.

#### References

- Ainsworth, T.D., Heron, S.F., Ortiz, J.C., Mumby, P.J., Grech, A., Ogawa, D., Eakin, C.M., Leggat, W., 2016. Climate change disables coral bleaching protection on the Great Barrier Reef. *Science* (80-) 352, 338–342.
- Bainbridge, S.J., 2017. Temperature and light patterns at four reefs along the Great Barrier Reef during the 2015–2016 austral summer: understanding patterns of observed coral bleaching. *J. Oper. Oceanogr.* 10, 16–29.
- Barshis, D.J., Birkeland, C., Toonen, R.J., Gates, R.D., Stillman, J.H., 2018. High-frequency temperature variability mirrors fixed differences in thermal limits of the massive coral *Porites lobata* (Dana, 1846). *J. Exp. Biol.* 221: Birkner P-C (2017) brms: an R Package for Bayesian Multilevel Models Using Stan. *J. Stat. Software* 80, 1–28.
- Bürkner, P-C, 2017. brms: An R Package for Bayesian multilevel models using Stan. *J. Stat. Softw.* 80, 1–28.
- Burn, D., Hoey, A.S., Matthews, S., Harrison, H.B., Pratchett, M.S., 2023. Differential bleaching susceptibility among coral taxa and colony sizes, relative to bleaching severity across Australia's Great Barrier Reef and Coral Sea Marine Parks. *Mar. Pollut. Bull.* 191, 114907.
- Chow, M.H., Tsang, R.H.L., Lam, E.K.Y., Ang, P., 2016. Quantifying the degree of coral bleaching using digital photographic technique. *J. Exp. Mar. Biol. Ecol.* 479, 60–68.
- DeCarlo, T.M., Cohen, A.L., Wong, G.T.F., Davis, K.A., Lohmann, P., Soong, K., 2017. Mass coral mortality under local amplification of 2 °C ocean warming. *Sci. Rep.* 7, 44586.
- Dietzel, A., Connolly, S.R., Hughes, T.P., Bode, M., 2021. The spatial footprint and patchiness of large-scale disturbances on coral reefs. *Global Change Biol.* 27, 4825–4838.
- Edmunds, P.J., 2005. The effect of sub-lethal increases in temperature on the growth and population trajectories of three scleractinian corals on the southern Great Barrier Reef. *Oecologia* 146, 350–364.
- Green, R.H., Lowe, R.J., Buckley, M.L., Foster, T., Gilmour, J.P., 2019. Physical mechanisms influencing localized patterns of temperature variability and coral bleaching within a system of reef atolls. *Coral Reefs* 38, 759–771.
- Grimaldi, C.M., Lowe, R.J., Benthuisen, J.A., Cuttler, M.V.W., Green, R.H., Gilmour, J.P., 2023. Hydrodynamic and atmospheric drivers create distinct thermal environments within a coral reef atoll. *Coral Reefs* 42, 693–706.
- 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, 713–719.
- Holbrook, S.J., Adam, T.C., Edmunds, P.J., Schmitt, R.J., Carpenter, R.C., Brooks, A.J., Lenihan, H.S., Briggs, C.J., 2018. Recruitment drives spatial variation in recovery rates of resilient coral reefs. *Sci. Rep.* 8, 7338.
- Hughes, T.P., Jackson, J.B.C., 1985. Population dynamics and life histories of foliaceous corals. *Ecol. Monogr.* 55, 141–166.
- Hughes, T.P., Kerry, J.T., Connolly, S.R., Álvarez-Romero, J.G., Eakin, C.M., Heron, S.F., Gonzalez, M.A., Moneghetti, J., 2021. Emergent properties in the responses of tropical corals to recurrent climate extremes. *Curr. Biol.* 31, 5393–5399 e3.

- Klepac, C.N., Barshis, D.J., 2020. Reduced thermal tolerance of massive coral species in a highly variable environment. *Proc. R Soc. B Biol. Sci.* 287, 19–21.
- Klepac, C.N., Barshis, D.J., 2022. High-resolution in situ thermal metrics coupled with acute heat stress experiments reveal differential coral bleaching susceptibility. *Coral Reefs* 41, 1045–1057.
- Lenihan, H., Adjerooud, M., Kotchen, M., Hench, J., Nakamura, T., 2008. Reef structure regulates small-scale spatial variation in coral bleaching. *Mar. Ecol. Prog. Ser.* 370, 127–141.
- Lough, J.M., Anderson, K.D., Hughes, T.P., 2018. Increasing thermal stress for tropical coral reefs: 1871–2017. *Sci. Rep.* 8, 6079.
- Loya, Y., Sakai, K., Yamazato, K., Nakano, Y., Sambali, H., Van Woesik, R., 2001. Coral bleaching: the winners and the losers. *Ecol. Lett.* 4, 122–131.
- McClanahan, T., Darling, E., Maina, J., Muthiga, N., D'agata, S., Leblond, J., Arthur, R., Jupiter, S., Wilson, S., Mangubhai, S., Ussi, A., Guillaume, M., Humphries, A., Patankar, V., Shedrawi, G., Pagu, J., Grimsditch, G., 2020. Highly variable taxa-specific coral bleaching responses to thermal stresses. *Mar. Ecol. Prog. Ser.* 648, 135–151.
- Morais, J., Morais, R., Tebbett, S.B., Bellwood, D.R., 2022. On the fate of dead coral colonies. *Funct. Ecol.* 36, 3148–3160.
- Morais, J., Morais, R.A., Tebbett, S.B., Pratchett, M.S., Bellwood, D.R., 2021. Dangerous demographics in post-bleach corals reveal boom-bust versus protracted declines. *Sci. Rep.* 11, 18787.
- Morais, J., Tebbett, S.B., Morais, R.A., Bellwood, D.R., 2023. **Natural Recovery of Corals after Severe Disturbance**, pp. 1–12. <https://doi.org/10.1111/ele.14332>.
- Pisapia, C., Burn, D., Pratchett, M.S., 2019. Changes in the population and community structure of corals during recent disturbances (February 2016–October 2017) on Maldivian coral reefs. *Sci. Rep.* 9, 8402.
- Pratchett, M.S., McCowan, D., Maynard, J.A., Heron, S.F., 2013. Changes in bleaching susceptibility among corals subject to ocean warming and recurrent bleaching in Moorea, French Polynesia. *PLoS One* 8, e70443.
- Pratchett, M.S., McWilliam, M.J., Riegl, B., 2020. Contrasting shifts in coral assemblages with increasing disturbances. *Coral Reefs* 39, 783–793.
- Rogers, J.S., Monismith, S.G., Koweek, D.A., Torres, W.I., Dunbar, R.B., 2016. Thermodynamics and hydrodynamics in an atoll reef system and their influence on coral cover. *Limnol. Oceanogr.* 61, 2191–2206.
- Safaie, A., Silbiger, N.J., McClanahan, T.R., Pawlak, G., Barshis, D.J., Hench, J.L., Rogers, J.S., Williams, G.J., Davis, K.A., 2018. High frequency temperature variability reduces the risk of coral bleaching. *Nat. Commun.* 9, 1671.
- Schmidt, G.M., Wall, M., Taylor, M., Jantzen, C., Richter, C., 2016. Large-amplitude internal waves sustain coral health during thermal stress. *Coral Reefs* 35, 869–881.
- Schneider, C.A., Rasband, W.S., Eliceiri, K.W., 2012. NIH Image to ImageJ: 25 years of image analysis. *Nat. Methods* 9, 671–675.
- Shenkar, N., Fine, M., Loya, Y., 2005. Size matters: bleaching dynamics of the coral *Oculina patagonica*. *Mar. Ecol. Prog. Ser.* 294, 181–188.
- Storlazzi, C.D., Cheriton, O.M., van Hooidonk, R., Zhao, Z., Brainard, R., 2020. Internal tides can provide thermal refugia that will buffer some coral reefs from future global warming. *Sci. Rep.* 10, 13435.
- Sully, S., Burkepille, D.E., Donovan, M.K., Hodgson, G., van Woesik, R., 2019. A global analysis of coral bleaching over the past two decades. *Nat. Commun.* 10, 1264.
- Team, R.C., 2020. R: A Language and Environment for Statistical Computing.
- Team, S.D., 2021. RStan: the R Interface to Stan. R Package version 2.21.2. <http://mc-stan.org/>.
- Tebbett, S.B., Morais, J., Bellwood, D.R., 2022a. Spatial patchiness in change, recruitment, and recovery on coral reefs at Lizard Island following consecutive bleaching events. *Mar. Environ. Res.* 173, 105537.
- Tebbett, S.B., Streit, R.P., Morais, J., Schlaefer, J.A., Swan, S., Bellwood, D.R., 2022b. Benthic cyanobacterial mat formation during severe coral bleaching at Lizard Island: the mediating role of water currents. *Mar. Environ. Res.* 181, 105752.
- Van Woesik, R., Houk, P., Isechal, A.L., Idechong, J.W., Victor, S., Golbuu, Y., 2012a. Climate-change refugia in the sheltered bays of Palau: analogs of future reefs. *Ecol. Evol.* 2, 2474–2484.
- Van Woesik, R., Irikawa, A., Anzai, R., Nakamura, T., 2012b. Effects of coral colony morphologies on mass transfer and susceptibility to thermal stress. *Coral Reefs* 31, 633–639.
- Vercelloni, J., Liqueur, B., Kennedy, E.V., González-Rivero, M., Caley, M.J., Peterson, E.E., Puotinen, M., Hoegh-Guldberg, O., Mengersen, K., 2020. Forecasting intensifying disturbance effects on coral reefs. *Global Change Biol.* 26, 2785–2797.
- Wagner, D.E., Kramer, P., Woesik, R., Van, 2010. Species composition, habitat, and water quality influence coral bleaching in southern Florida. *Mar. Ecol. Prog. Ser.* 408, 65–78.
- Wismer, S., Tebbett, S.B., Streit, R.P., Bellwood, D.R., 2019. Spatial mismatch in fish and coral loss following 2016 mass coral bleaching. *Sci. Total Environ.* 650, 1487–1498.
- Wyatt, A.S.J., Leichter, J.J., Toth, L.T., Miyajima, T., Aronson, R.B., Nagata, T., 2020. Heat accumulation on coral reefs mitigated by internal waves. *Nat. Geosci.* 13, 28–34.