Coral Reefs (2025) 44:1419–1426
https://doi.org/10.1007/s00338-025-02639-4

BRIEF REPORT

Impact of wave exposure on bleaching of large benthic foraminifera

Claire E. Reymond[1,2,4] · **Caroline Romo**[4] · **Gabija Posiunaite**[4] · **Maria Byrne**[1,2,3] · **Jody M. Webster**[4]

Received: 11 September 2024 / Accepted: 24 February 2025 / Published online: 12 May 2025

Abstract During the 2024 global mass bleaching event, a rapid bleaching assessment was conducted on two large benthic foraminifera populations on One Tree Reef, southern Great Barrier Reef. In tropical reef ecosystems, large benthic foraminifera are major carbonate sediment producers and function as important ecological engineers. We documented the thermal stress of *Marginopora vertebralis* and *Baculogypsina sphaerulata* from two high-density populations along the leeward and windward side of One Tree Reef in March 2024 following an 8-degree heating week with local on-reef temperatures exceeding 30 °C. Bleaching was more prevalent at the lower-energy leeward site (81.4% of *M. vertebralis* and 80.2% of *B. sphaerulata* individuals bleached, respectively) than the windward site (31.1% of *M. vertebralis* and 40.8% of *B. sphaerulata* bleached), suggesting localised hydrodynamic exposure has a significant impact on the health and bleaching susceptibility of benthic foraminifera. This study provides a rapid bleaching guide and emphasises the necessity of ongoing monitoring of benthic foraminifera to understand local and regional impacts of climate-induced stressors on reef carbonate production.

Keywords Marine heat waves · Bleaching · Hydrodynamics · Reef monitoring

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s00338-025-02639-4.

✉ Claire E. Reymond
claire.reymond@sydney.edu.au

1 School of Life and Environmental Sciences, The University of Sydney, Sydney, NSW 2006, Australia

2 Marine Studies Institute, The University of Sydney, Sydney, NSW 2006, Australia

3 Marine Biology and Aquaculture, The College of Science and Engineering, James Cook University Townsville, Townsville, QLD 4811, Australia

4 Geocoastal Research Group, School of Geosciences, The University of Sydney, Sydney, NSW 2006, Australia

Introduction

Marine heatwaves are becoming more frequent and prolonged due to anthropogenic greenhouse gas emissions (Hobday et al. 2018; Schmidt et al. 2011). The global mass coral bleaching event in early 2024 marked the Great Barrier Reef's (GBR) seventh event since 1998 and the fifth since 2016. Satellite and aerial surveys in 2024 showed extreme ocean temperatures and extensive coral bleaching across all regions (north, central, and south) of the GBR (Cantin et al. 2024). The southern region, including the highly protected One Tree Reef (OTR), suffered severe coral bleaching and mortality following prolonged ocean warming exceeding 30 °C and 8-degree heating week (DHW) (Byrne et al. 2025). Since the major coral bleaching events in 2016 and 2017, the Southern Great Barrier Reef, including OTR, has not experienced significant bleaching, with only low-level bleaching (< 10% of colonies) observed in 2021 (Emslie 2021; Cantin et al. 2024).

More research is needed to assess the implications of marine heat waves on other non-coral marine carbonate producers, such as large benthic foraminifera (LBF). These organisms contribute significantly to the carbonate sediment budget within reef systems (Hallock 1981; Langer et al. 1997; Hohenegger 2006; Doo et al. 2017) and function as key ecological engineers (Dawson et al. 2014). The sand produced by LBF shapes coastal shorelines and habitats, and provides coastal stabilisation (Fellows et al 2017). In the southern

Great Barrier Reef, LBF contribute approximately 3 kg $CaCO_3$ m^{-2} y^{-1} and 32% of the reef sediments in the sand aprons in OTR (Doo et al. 2014; Fellowes et al. 2017). Populations of *Marginopora* in the subtropical northwest Pacific contribute approximately 5 kg CaCO3 m^{-2} yr^{-1} to the reef sediments (Fujita et al. 2000), which is higher than the estimated global average of 0.03–1 kg $CaCO_3$ m^{-2} y^{-1} (Langer et al. 1997). Other studies, such as Hallock (1981) and Doo et al. (2017), have provided similar estimates for different species of foraminifera, highlighting the significant contribution of these organisms to carbonate production in reef ecosystems. In the western Pacific, studies on LBF have reported an average lifespan of 17 months and the presence of multiple modes of reproduction (Fujita et al. 2000; Hohenegger 2006; Hosono et al. 2013; Hohenegger et al. 2019). Despite their importance, bleaching patterns of LBF are less understood than other photosymbiotic reef organisms (Narayan et al. 2022). This highlights the need to include LBF in long-term and continuous reef health initiatives.

The capacity of LBF to prolifically produce calcium carbonate exoskeleton ($CaCO_3$ tests) is in part due to their obligatory symbioses with photosynthetic microalgae, such as diatoms, rhodophytes, chlorophytes, and/or zooxanthellae-dinoflagellates (Lee and Hallock 1987; Lee 2006). Within a single LBF species, these photosymbionts have high genetic diversity (Momigliano and Uthicke 2013; Prazeres et al. 2021; Stuhr et al. 2021), enhancing their potential adaptability to environmental stressors (Stuhr et al. 2017, 2018).

Bleaching in foraminifera was initially documented in *Amphistegina gibbosa* from the Florida Keys (Hallock et al. 1993; Hallock 2000), and here, we present the first report of bleaching in LBF in the GBR. Experimental studies suggest that the thermal threshold for optimal physiological function in LBF is 30 °C (Talge and Hallock 1995, 2003; Fujita et al. 2014; Schmidt et al. 2014; Stuhr et al. 2017, 2018), as indicated by significant declines in calcification (Schmidt et al. 2011, 2014; Doo et al. 2012; Pinko et al. 2020) and reproduction (Hohenegger et al. 2019; Hallock and Reymond 2022; Reymond et al. 2022). The response to thermal stress can vary among LBF species, likely due to differences in local physicochemical conditions and the ability to acclimatise in different cross-shelf habitats (Doo et al. 2014; Fujita et al. 2014; Prazeres et al. 2016; Kenigsberg et al. 2022) or through evolutionary adaptation (Schmidt et al. 2016; Stuhr et al. 2021).

With marine heatwaves becoming more frequent and prolonged (Hobday et al. 2018), there is an increasing need to understand the impact of thermal stress on LBF populations. We documented the thermal stress response of two prominent LBF species, *Marginopora vertebralis* (a dinoflagellate endosymbiont-bearing porcelaneous foraminifera)

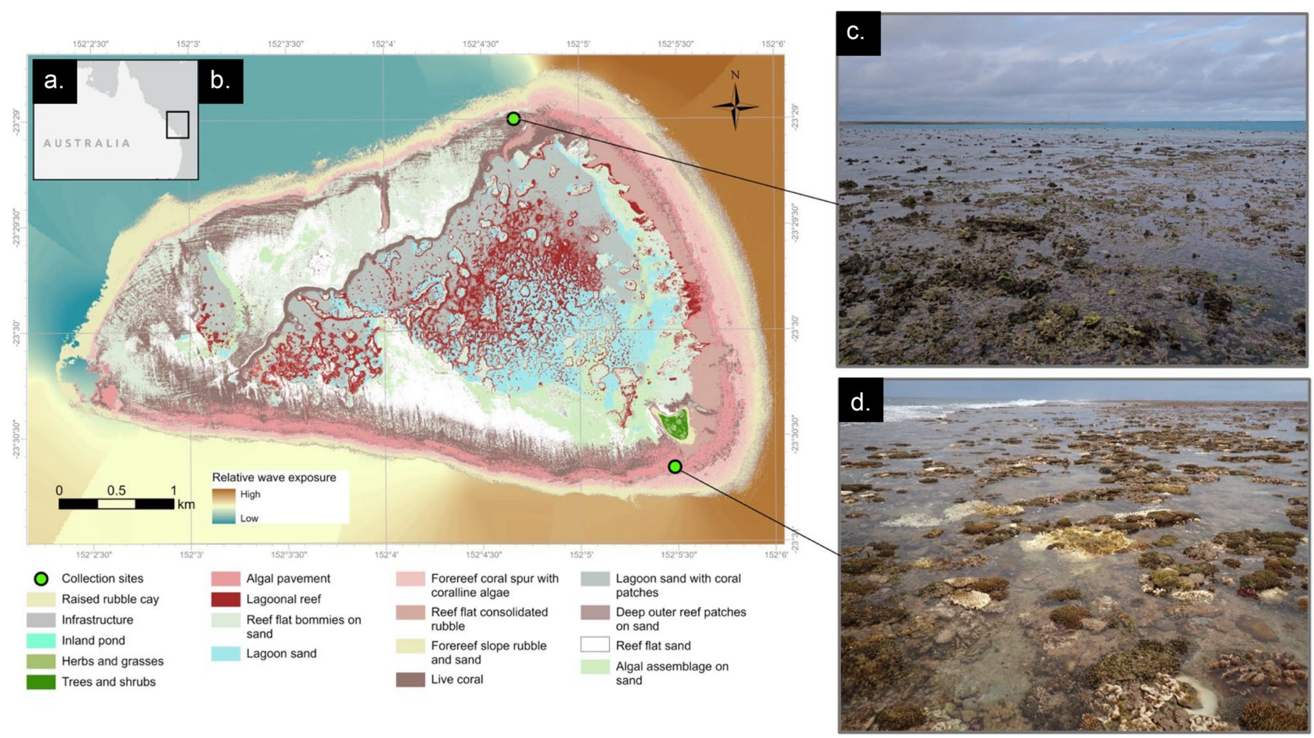

Fig. 1 Map of **a** Capricorn Bunker Group 100 km off the Australian mainland in the Great Barrier Reef. **b** Benthic-type map of One Tree Reef (OTR), adapted from Hamylton et al. (2013), and relative wave exposure (GREMO) (Pepper and Puotinen 2009). Collection sites are indicated with in situ images of relative microhabitat. Samples were collected from two coral–algal fore reef locations: **c** the northern leeward zone and **d** the southern windward zone

and *Baculogypsina sphaerulata* (a diatom endosymbiont-bearing hyaline foraminifer), across One Tree Reef's leeward and windward coral–algal reef flats during the 2024 marine heatwave that caused mass bleaching in corals (Cantin et al. 2024).

Methods and materials

One Tree Reef (OTR) is located 100 km off the Australian mainland in the Capricorn Bunker Group. For 40 years, it has had the highest level of protection (Scientific Zone) in the GBR World Heritage Area. OTR is a tide-depended system, in which the leeward (northern) and windward (southern) sides of the reef experience different hydrodynamic exposures (Pepper and Puotinen 2009; Duce et al. 2020). Samples of LBF were collected from two coral reef sand aprons (Fig. 1): the northern leeward zone (23°29′00″ S, 152°04′40″ E) and the southern windward zone (23°30′39″ S, 152°05′29″ E). These sites, accessible at low tide, serve as the primary sources of carbonate sediment for the lagoon (Doo et al. 2012; Vila-Concejo et al. 2022; Bauder et al. 2023) and have up to one-third foraminifera content (Fellowes et al. 2017).

One Tree Lagoon reached Alert Level 1, equivalent to 4-DHW on January 24 and Alert Level 2 on February 8 (8-DHW), with local on-reef temperature sensors recording a peak of 30.55 °C (Byrne et al. 2025). Edging closer to extreme heatwaves earlier than anticipated, sea surface temperature (SST) in the upper range of 30 °C and 32 °C

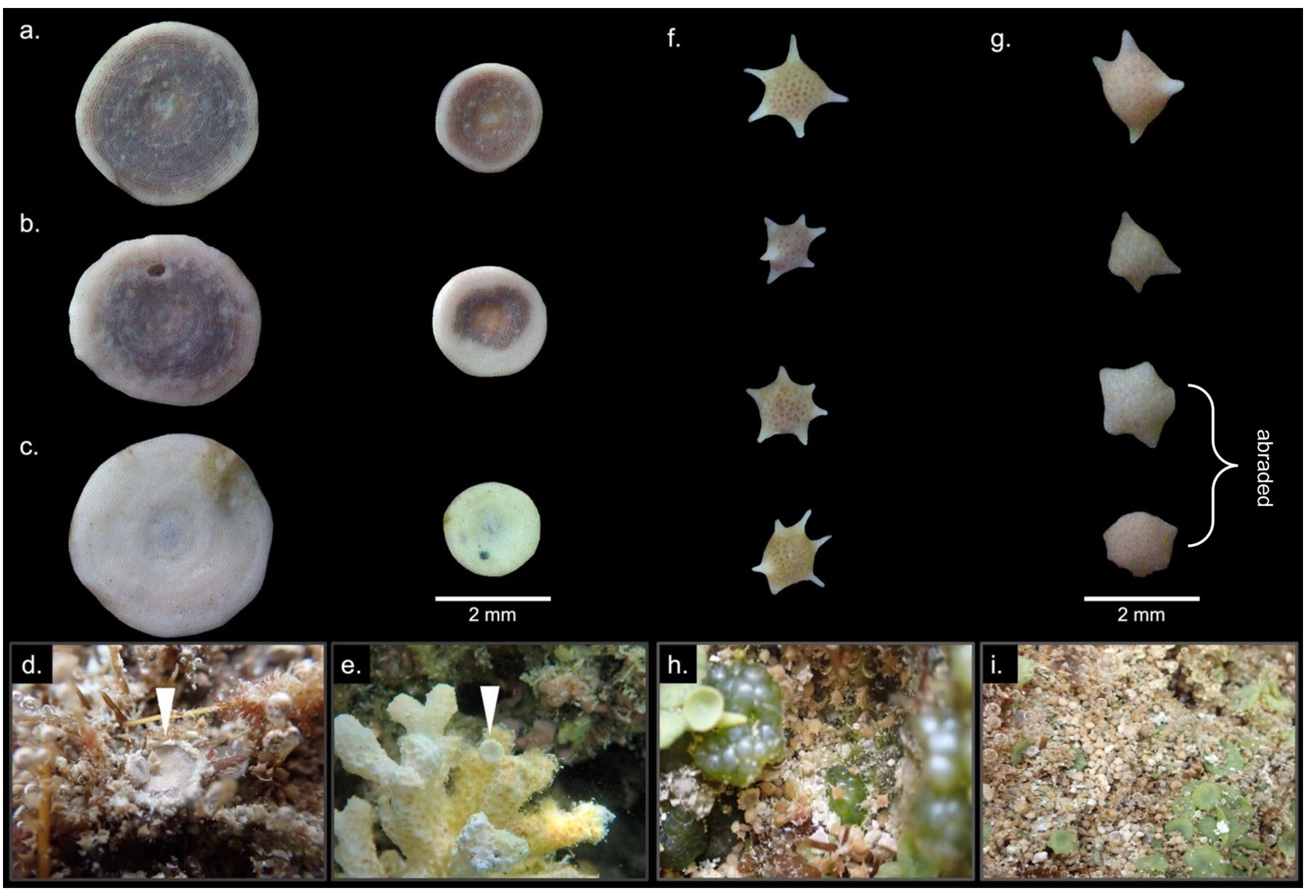

Fig. 2 Thermal stress chart of *M. vertebralis* and *B. sphaerulata*, the 2 mm scale bar is consistence for all individual images of the foraminifera. **a–e** *M. vertebralis* sorted into size classes left, > 2 mm; right, ≤ 2 mm. **a** Healthy: active pseudopodia with retention of endosymbionts noted by the robust pigmentation of brown/purple hues and a thin white ring around the aperture of the test. **b** Mottled: weakly retained endosymbiont, possible abrasion of test and patchy pigmentation. **c** Bleached: complete loss of endosymbiont, no visible pigmentation little t no abrasion. **d** Healthy *M. vertebralis* attached to turfing algae. **e** In situ bleached *M. vertebralis* attached to bleached coral. Thermal stress chart of *B. sphaerulata* (**f–i**) sorted by **f** Healthy: active pseudopodia, intact radial spines, robust brown/orange pigmentation, and visibly punctuated chambers. **g** Bleached; non-active pseudopodia radial spines in tack, loss of endosymbiont indicated by reduced pigmentation, including examples of abraded *B. sphaerulata*, which were excluded from the analysis. **h** Healthy individuals located within the turf algal pavement compared to **i** bleached and abraded tests. Individuals from both species with extensive abrasion and/or covered in epiphytes were excluded from the analysis because to timing of the death likely occurred prior to the heatwave

is in line with the IPCC upper projections (A1F) for 2100 (Meehl et al. 2007).

Samples of *Marginopora vertebralis* and *Baculogypsina sphaerulata* were systematically collected from forty 50 cm^2 quadrats (twenty samples of each species along each reef site). Collection sites were located on the crustose coralline (*Porolithion onkodes*) dominated coral–algal reef pavements, which were also covered with various calcifying, filamentous, and turfing algae, e.g. *Halimeda spp., Laurencia spp., Caulerpa racemosa* (*c.f.* Borowitzka and Larkum 1986). In each quadrat, the first 100 individuals of each species encountered were collected. However, some quadrats on the leeward reef flat contained fewer than 100 M. *vertebralis* individuals; in these cases, the maximum number available were collected, in total 3,430 individuals were assessed. Samples were collected and rapidly assessed at low tide over four consecutive days, ensuring consistent tidal conditions and no unusual wave action. Grids were carefully selected in areas with stable water coverage. To minimise disturbance, foraminifera were collected in situ using a fine brush to gently remove them from turf algae without damaging the substrate, ensuring the unbiased collection of both recently dead and living samples. Specimens were carefully sorted, with movement of living individuals observed, and photographed in both the field and post-sorting under low light conditions. Samples were collected into sealed containers with natural seawater and transported back to the water laboratory at the research station in an insulated bag to reduce light exposure and maintain stable ambient temperatures. Samples were stored in separate vials to examine pseudopodia activity, to distinguish between living and dead individuals, and scored based on the extent of visible pigment loss. Precautions were also taken to minimise handling and light exposure during pigment checks to reduce potential bleaching effects. Taxonomic identifications were conducted following Hayward et al. (2025) and Uthicke and Nobes (2008) using a digital Zeiss STEMI 305 microscope with an attached camera.

A health chart for *M. vertebralis* and *B. sphaerulata* was developed and used to assign individuals into specific categories (Fig. 2). Healthy specimens of *M. vertebralis* exhibited an even brown/purple hue with a thin white ring along the aperture, while healthy *B. sphaerulata* displayed an orange/brown hue with intact radial spines. Individuals of *M. vertebralis* with slight purple or brown hues and thick white bands or patches were categorised as mottled. Mobility was also observed among individuals that were healthy or mottled. Pale individuals with pigment loss (photosymbiont damage) and no abraded individuals

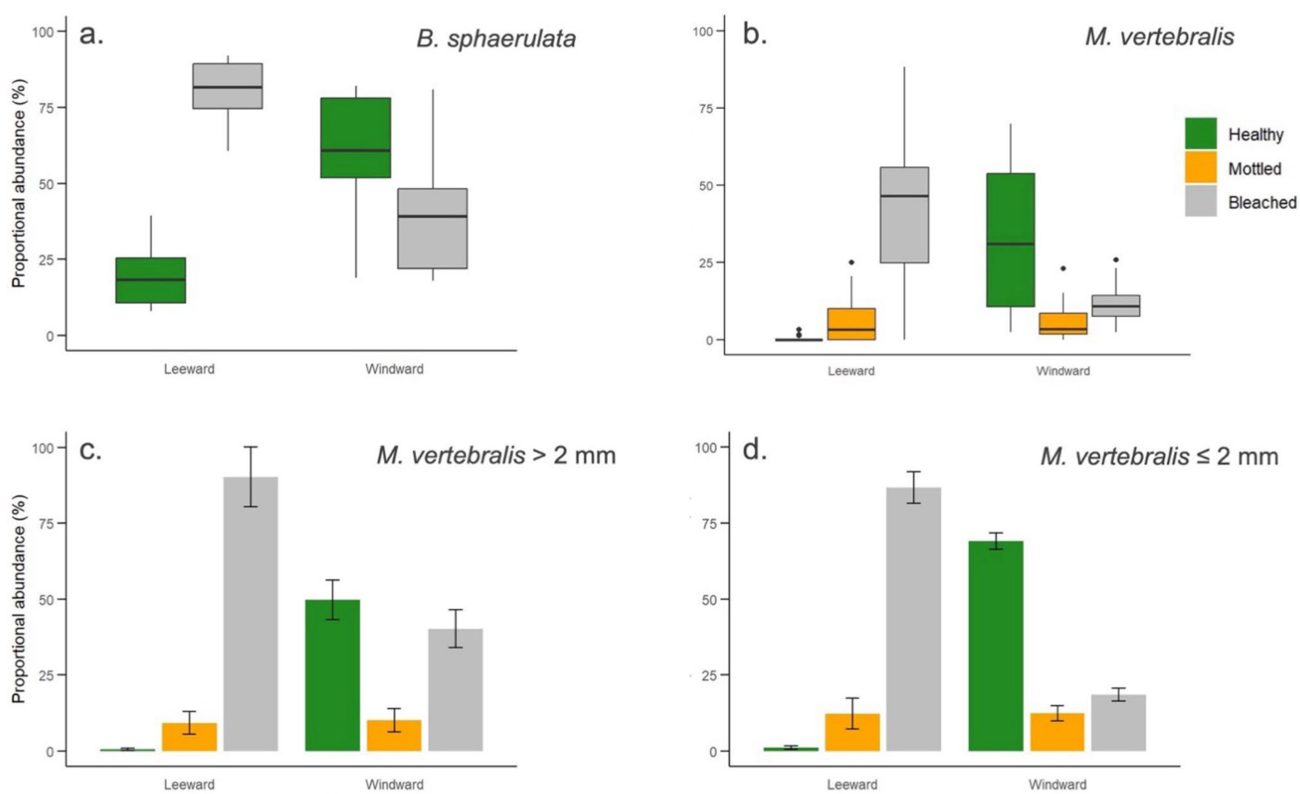

Fig. 3 Response of *M. vertebralis* and *B. sphaerulata* from One Tree Reef, indicating there is a greater thermal stress in the northern leeward coral–algal reef flat. Overall proportional abundance of bleaching in *M. vertebralis* and *B. sphaerulata* (**a**, **b**). Bleach levels of **c** large (> 2 mm) and **d** small (≤ 2 mm) *M. vertebralis* are categorised by size to reflect different life cycle stages

Table 1 Chi-squared tests contingency table assessing the effects of location on the health status of *M. vertebralis* and *B. sphaerulata* populations. The health status distribution significantly differs (*p*-value < 0.001) between the two sites, suggesting that location is an important factor influencing the thermal stress response of *M. vertebralis* and *B. sphaerulata*

	Baculogypsina sphaerulata		Marginopora vertebralis								
	Percentage		*Percentage (ALL)*			*Percentage (Small)*			*Percentage (Large)*		
	Healthy	Bleached	Healthy	Mottled	Bleached	Healthy	Mottled	Bleached	Healthy	Mottled	Bleached
Leeward	19.75	80.25	0.94	11.28	87.78	1.12	12.29	86.59	0.57	9.20	90.23
Windward	59.17	40.83	64.96	11.94	23.10	69.02	12.45	18.53	49.74	10.05	40.21
	Count		*Count (ALL)*			*Count (Small)*			*Count (Large)*		
	Healthy	Bleached	Healthy	Mottled	Bleached	Healthy	Mottled	Bleached	Healthy	Mottled	Bleached
Leeward	182	769	5	60	467	4	44	310	1	16	157
Windward	592	459	582	107	207	488	88	131	94	19	76
Chi-squared test of independence											
χ^2	30.90		99.98			106.79			17.37		
df	1		2			2			2		
p-value	< 0.001		< 0.001			< 0.001			< 0.001		

from both species were considered recently dead and classified as bleached. Encrusted and highly abraded individuals were excluded from the analysis as the time of death likely occurred prior to the heatwave. Test abrasion was determined by radial spine or prolocular alteration. The size class distribution for *M. vertebralis* was divided into two categories based on test diameter: those with a diameter of ≤ 2 mm and those with a diameter of > 2 mm. This classification was used to capture two distinct cohorts and ensure that age was considered. Conversely, the test size for *B. sphaerulata* was uniform, so no size-based classification was necessary.

The benthic cover types were mapped in ArcGIS Pro 3.3 by adapting the reef zonation classifications from Hamylton et al. (2013). In combination, GREMO (Generic Model for Estimating Relative Wave Exposure) was overlayed as a visual representation of wave exposure, highlighting the differences between the leeward and windward reef zones at OTR (Pepper and Puotinen 2009). While we recognise that these data may not fully capture the nuances of intertidal hydrodynamics, they represent the most accurate and comprehensive datasets currently available. Since the dataset is categorical in nature, the chi-squared test of independence, analysed in R Studio, was used to test the health status of each species from two wave exposure locations. Moreover, the residuals, diagnostic, and plots were made using the statistical package (lme4) as a GLMM general linear model were examined to ensure model fit and normality (Fig. S1).

Results and discussion

After experiencing an 8-DWH with local on-reef temperatures exceeding 30 °C (Byrne et al. 2025), it is evident both the northern and southern coral–algal reef zones on OTR were seriously impacted by the prolonged marine heatwave on OTR in 2024. Even with their morphological and physiological differences (Fig. 2), *M. vertebralis* and *B. sphaerulata* both exhibited similar thermal stress patterns in the shallow coral–algal reef flat of OTR. Nonetheless, populations of *M. vertebralis* and *B. sphaerulata* from the northern leeward coral–algal reef flat on OTR showed greater thermal stress (Fig. 3; Table 1). Approximately 80% of all *B. sphaerulata* was bleached in the leeward site compared to ~ 40% of individuals in the windward site. Even though high intensity bleaching was observed at each site, the chi-squared of independence suggests a higher bleaching trend associated with lower wave exposure ($p < 0.01$) for both *M. vertebralis* and *B. sphaerulata* (Table 1). The removal and transport of dead epiphytic foraminiferal shells by wave energy is a plausible mechanism influencing observed bleaching patterns, particularly over longer timescales (years to decades), as evidenced by test abrasion in high hydrodynamic environments (Fellowes et al. 2017). These findings suggest the windward (southern) reef flat, which experiences greater hydrodynamic exposure (Pepper and Puotinen 2009; Duce et al. 2020), has the potential to create and support thermal refuges as observed with internal waves at depths in coral reefs (Wyatt et al. 2020).

While this is a rapid assessment of the response of LBF to heatwave conditions on one reef, the implications for carbonate sediment production and biodiversity on a larger regional or global scale are serious. Previous studies have shown the impacts of temperature on *M. vertebralis* growth from OTR were evident at 2 °C above ambient conditions (28 °C) with a 130% decline in $CaCO_3$ production at 32 °C (Doo et al. 2012). Similarly, studies along a natural temperature and nutrient gradient in the GBR indicated the average summer temperature of 28 °C is near the upper limit before the onset of thermal stress for *M. vertebralis* (Reymond et al. 2011).

Shifting habitats and range potentials of LBF due to climate change will significantly impact biodiversity and carbonate budgets. Future studies will benefit from additional monitoring of the transport and fate of detached shells in different hydrodynamic conditions to further refine our understanding of the influence of hydrodynamics on the bleaching intensity of LBF. Even though the unique conditions at OTR influenced our decision to use a north–south sampling design, an east–west sampling approach could also capture differences between coasts with varying hydrodynamic regimes. This rapid in-field bleaching guide (Fig. 2) can be applied globally to understand reef population dynamics and sediment budgets of foraminifera. This guide can be applied in other monitoring sites to gauge the effect of marine heat waves along with additional parameters such as PAM fluorometry, chlorophyll-a concentration, and proteomic analyses (e.g. Talge and Hallock 2003; Schmidt et al. 2011; Stuhr et al. 2021) to understand the overall health and potential climate adaptation of LBF.

Acknowledgements This research was funded by the Australian Research Council Discovery Program ARC-DP220101125 (M.B). C.E.R is funded by Geoscience Australia (Australian Government) and the School of Geosciences, University of Sydney. Support to JMW was provided by the Hanse-Wissenschaftskolleg (HWK) Institute for Advanced Study, Delmenhorst, Germany. The authors declare that they have no conflict of interest. We acknowledge students from the Coral Reefs and Climate Change MARS5007 course Indi Cohen, Georgia Dorahy, and Makayla Oosterbeek, as well as the One Tree Island Research Station managers Ruby Holmes and Heinrich Breuer for their assistance.

Author contributions C.E.R. and C.R. conceived the study and designed the methodology. C.R. and G.P. conducted fieldwork and data analysis. C.E.R. contributed to statistical validation and visualisation. All authors contributed to writing and editing the manuscript. Supervision and funding acquisition were led by C.E.R, J.M.W, and M.B.

Funding Open Access funding enabled and organized by CAUL and its Member Institutions. Geoscience Australia (Australian Government), School of Geosciences, The University of Sydney, Australian Research Council Discovery Program, ARC-DP220101125, Hanse-Wissenschaftskolleg (HWK) Institute for Advanced Study, Delmenhorst, Germany.

Data availability Data is provided within the manuscript or supplementary information files.

Declarations

Conflict of interest The authors declare no competing interests.

References

Bauder Y, Mamo B, Brock Glenn A, Kosnik Matthew A (2023) One tree reef foraminifera: a relic of the pre-colonial Great Barrier Reef. Geol Soc London Spec Publ 529:175–193

Borowitzka MA, Larkum AWD (1986) Reef algae. Oceanus Int Mag Marine Sci Policy 29:49–54

Byrne M, Waller A, Clements M, Kelly AS, Kingsford MJ, Liu B, Reymond CE, Vila-Concejo A, Webb M, Whitton K, Foo SA (2025) Catastrophic bleaching in protected reefs of the Southern Great Barrier Reef. Limnol Oceanogr Lett. https://doi.org/10.1002/lol2.10456

Cantin N, James N, Stella J (2024) Aerial surveys of the 2024 mass coral bleaching event on the Great Barrier Reef Great Barrier Reef Marine Park authority (GBRMPA), Townsville

Dawson JL, Smithers SG, Hua Q (2014) The importance of large benthic foraminifera to reef island sediment budget and dynamics at Raine Island, northern Great Barrier Reef. Geomorphology 222:68–81

Doo SS, Hamylton S, Byrne M (2012) Reef-scale assessment of intertidal large benthic foraminifera populations on one tree Island, great barrier reef and their future carbonate production potential in a warming ocean. Zool Stud 51:1298–1307

Doo SS, Fujita K, Byrne M, Uthicke S (2014) Fate of calcifying tropical symbiont-bearing large benthic foraminifera: living sands in a changing ocean. Biol Bull 226:169–186

Doo SS, Hamylton S, Finfer J, Byrne M (2017) Spatial and temporal variation in reef-scale carbonate storage of large benthic foraminifera: a case study on One Tree Reef. Coral Reefs 36:293–303

Duce S, Dechnik B, Webster JM, Hua Q, Sadler J, Webb GE, Nothdurft L, Salas-Saavedra M, Vila-Concejo A (2020) Mechanisms of spur and groove development and implications for reef platform evolution. Quatern Sci Rev 231:106155

Emslie M (2021) Reef in recovery window after decade of disturbances long-term monitoring program - annual summary report of Coral Reef condition 2020/21. Australian Insitute of Marine Science

Fellowes TE, Gacutan J, Harris DL, Vila-Concejo A, Webster JM, Byrne M (2017) Patterns of sediment transport using foraminifera tracers across sand aprons on the Great Barrier Reef. J Coastal Res 33:864–873

Fujita K, Nishi H, Saito T (2000) Population dynamics of marginopora kudakajimensis gudmundsson (Foraminifera: Soritidae) in the Ryukyu Islands, the subtropical northwest Pacific. Mar Micropaleontol 38:267–284

Fujita K, Okai T, Hosono T (2014) Oxygen metabolic responses of three species of large benthic foraminifers with algal symbionts to temperature stress. PLoS ONE 9:e90304

Hallock P (1981) Production of carbonate sediments by selected large benthic foraminifera on two Pacific coral reefs. J Sediment Petrol 51:467–474

Hallock P (2000) Symbiont-bearing foraminifera: harbingers of global change. Micropaleontology 46:95–104

Hallock P, Reymond CE (2022) Contributions of trimorphic life cycles to dispersal and evolutionary trends in large benthic foraminifers. Journal of Earth Science 33:1425–1433

Hallock P, Talge HK, Smith KM, Cockey EM (1993) Bleaching in a reef-dwelling Foraminifera *Amphistegina gibbosa*. In: Proceedings of the 7th international Coral Reef symposium, pp 44–49

Hayward BW, Le Coze F, Vachard D, Gross O (2025) World foraminifera database.

Hobday AJ, Oliver ECJ, Sen Gupta A, Benthuysen JA, Burrows MT, Donat MG, Holbrook NJ, Moore PJ, Thomsen MS, Wernberg T, Smale DA (2018) Categorizing and naming marine heatwaves. Oceanography 31:162–173

Hohenegger J (2006) The importance of symbiont-bearing benthic foraminifera for West Pacific carbonate beach environments. Mar Micropaleontol 61:4–39

Hohenegger J, Kinoshita S, Briguglio A, Eder W, Wöger J (2019) Lunar cycles and rainy seasons drive growth and reproduction in nummulitid foraminifera, important producers of carbonate buildups. Sci Rep 9:8286

Hosono T, Lopati P, Kayanne H (2013) Estimation of the growth pattern of *Baculogypsina sphaerulata* (Foraminifera) in a tropical environment using a floating chamber method. J Exp Mar Biol Ecol 448:156–161

Kenigsberg C, Titelboim D, Ashckenazi-Polivoda S, Herut B, Kucera M, Zukerman Y, Hyams-Kaphzan O, Almogi-Labin A, Abramovich S (2022) The combined effects of rising temperature and salinity may halt the future proliferation of symbiont-bearing foraminifera as ecosystem engineers. Sci Total Environ 806:150581

Langer MR, Silk MT, Lipps JH (1997) Global ocean carbonate and carbon dioxide production: the role of reef foraminifera. J Foramin Res 27:271–277

Lee JJ (2006) Algal symbiosis in larger foraminifera. Symbiosis 42:63–75

Lee JJ, Hallock P (1987) Algal symbiosis as the driving force in the evolution of larger foraminiferaa. Ann N Y Acad Sci 503:330–347

Meehl GA, Stocker TF, Collins WD, Friedlingstein P, Gaye AT, Gregory JM, Kitoh A, Knutti R, Murphy JM, Noda A, Raper SCB, Watterson IG, Weaver AJ, Zhao Z-C (2007) Global climate projections. In: Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL (eds.), Climate change 2007: the physical science basis contribution of working group I to the fourth assessment report of the intergovernmental panel on climate change. Cambridge University Press, Cambridge, United Kingdom and New York, NY, USA,

Momigliano P, Uthicke S (2013) Symbiosis in a giant protist (Marginopora vertebralis, Soritinae): flexibility in symbiotic partnerships along a natural temperature gradient. Mar Ecol Prog Ser 491:33–46

Narayan GR, Reymond CE, Stuhr M, Doo S, Schmidt C, Mann T, Westphal H (2022) Response of large benthic foraminifera to climate and local changes: Implications for future carbonate production. Sedimentology 69:121–161

Pepper AR, Puotinen ML (2009) GREMO: a GIS-based generic model for estimating relative wave exposure

Pinko D, Abramovich S, Titelboim D (2020) Foraminiferal holobiont thermal tolerance under future warming – roommate problems or successful collaboration? Biogeosciences 17:2341–2348

Prazeres M, Uthicke S, Pandolfi JM (2016) Influence of local habitat on the physiological responses of large benthic foraminifera to temperature and nutrient stress. Sci Rep 6:21936

Prazeres M, Roberts TE, Ramadhani SF, Doo SS, Schmidt C, Stuhr M, Renema W (2021) Diversity and flexibility of algal symbiont community in globally distributed larger benthic foraminifera of the genus Amphistegina. BMC Microbiol. https://doi.org/10.1186/s12866-021-02299-8

Reymond CE, Uthicke S, Pandolfi JM (2011) Inhibited growth in the photosymbiont-bearing foraminifer Marginopora vertebralis from the nearshore Great Barrier Reef, Australia. Mar Ecol Prog Ser 435:97–109

Reymond CE, Patel F, Uthicke S (2022) Stable adult growth but reduced asexual fecundity in Marginopora vertebralis, under global climate change scenarios. Journal of Earth Science 33:1400–1410

Schmidt C, Heinz P, Kucera M, Uthicke S (2011) Temperature-induced stress leads to bleaching in larger benthic foraminifera hosting endosymbiotic diatoms. Limnol Oceanogr 56:1587–1602

Schmidt C, Kucera M, Uthicke S (2014) Combined effects of warming and ocean acidification on coral reef Foraminifera Marginopora vertebralis and Heterostegina depressa. Coral Reefs 33:805–818

Schmidt C, Titelboim D, Brandt J, Herut B, Abramovich S, Almogi-Labin A, Kucera M (2016) Extremely heat tolerant photo-symbiosis in a shallow marine benthic foraminifera. Sci Rep 6:30930

Stuhr M, Reymond CE, Rieder V, Hallock P, Hrer JRR, Westphal H, Kucera M (2017) Reef calcifiers are adapted to episodic heat stress but vulnerable to sustained warming. PLoS ONE 12:e0179753

Stuhr M, Meyer A, Reymond CE, Narayan GR, Rieder V, Rahnenführer J, Kucera M, Westphal H, Muhando CA, Hallock P (2018) Variable thermal stress tolerance of the reef-associated symbiont-bearing foraminifera Amphistegina linked to differences in symbiont type. Coral Reefs 37:811–824

Stuhr M, Cameron LP, Blank-Landeshammer B, Reymond CE, Doo SS, Westphal H, Sickmann A, Ries JB (2021) Divergent proteomic responses offer insights into resistant physiological responses of a reef-foraminifera to climate change scenarios. Oceans 2:281–314

Talge HK, Hallock P (1995) Cytological examination of symbiont loss in a benthic foraminifera, *Amphistegina gibbosa*. Marine Micropaleontol 26:107–113

Talge HK, Hallock P (2003) Ultrastructural responses in field-bleached and experimentally stressed Amphistegina gibbosa (Class Foraminifera). J Eukaryot Microbiol 50:324–333

Uthicke S, Nobes K (2008) Benthic foraminifera as ecological indicators for water quality on the Great Barrier Reef. Estuar Coast Shelf Sci 78:763–773

Vila-Concejo A, Hamylton SM, Webster JM, Duce SJ, Fellowes TE (2022) Lagoon infilling by coral reef sand aprons as a proxy for carbonate sediment productivity. Geology 50:1427–1431

Wyatt ASJ, Leichter JJ, Toth LT, Miyajima T, Aronson RB, Nagata T (2020) Heat accumulation on coral reefs mitigated by internal waves. Nat Geosci 13:28–34