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ARTICLE

Coastal and Marine Ecology

High survival following bleaching underscores the resilience of a frequently disturbed region of the Great Barrier Reef

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Abstract

Natural bleaching events provide an opportunity to examine how local-scale environmental variation influences bleaching severity and recovery. During the 2020 marine heat wave, we documented widespread and severe coral bleaching affecting 75%–98% of coral cover throughout the Keppel Islands in the southern inshore Great Barrier Reef. *Acropora*, *Pocillopora*, and *Porites* were the most severely affected genera, while *Montipora* was comparatively less susceptible. Site-specific heat-exposure metrics were not correlated with *Acropora* bleaching severity, but recovery was faster at sites that experienced lower heat exposure. Despite severe bleaching and exposure to accumulated heat that often results in coral mortality (degree heating weeks ~4–8), cover remained stable. Approximately 94% of fate-tracked *Acropora millepora* colonies survived, perhaps due to reduced irradiance stress from high turbidity, heterotrophic feeding, and large tidal flows that can increase mass transfer. Severe bleaching followed by rapid recovery and the continuing dominance of *Acropora* populations in the Keppel Islands is indicative of high resilience. These coral communities have survived a 0.8°C increase in average temperatures over the last 150 years. However, recovery following the 2020 bleaching was driven by the easing of thermal stress, which may challenge their recovery potential under further warming.

KEYWORDS
climate change, coral bleaching, coral reefs, currents, heat exposure, mortality, recovery, resilience, susceptibility, thermal stress, water flow

INTRODUCTION

Global warming has accelerated since 1981 with each new year increasingly likely to rank in the top 10 hottest years on record (National Oceanographic and Atmospheric Administration [NOAA], 2021). Oceans are warming, and coral reefs are increasingly experiencing both warmer summers and winters (NOAA, 2021). Marine heat waves bring periods of extreme temperatures and, particularly when combined with high irradiance, can disrupt the functioning of the coral holobiont and lead to bleaching (Baird et al., 2009; Bourne et al., 2008; Brown, 1987;

Downs et al., 2013; Hoegh-Guldberg, 1999; McClanahan et al., 2019). The frequency and intensity of marine heat waves, and subsequent coral-bleaching events, are increasing worldwide (Cai et al., 2014; Hoegh-Guldberg, 1999; Hughes et al., 2017; Timmermann et al., 1999) and have contributed to regional declines in coral cover and diversity (Baker et al., 2008; Bruno & Selig, 2007; De'ath et al., 2012; Gardner et al., 2003; Ortiz et al., 2018; Osborne et al., 2017; van Woesik et al., 2018). As a result, climate change-driven ocean warming is now considered to be the most significant threat to the persistence of globally functioning coral-reef ecosystems (Bellwood et al., 2004; Riegl et al., 2009), and the capacity for coral communities to continue to recover from more frequent and intense coral bleaching is diminishing (Baker et al., 2008; Donovan et al., 2021; Ortiz et al., 2018; van Woesik et al., 2018).

Although bleaching events impact reefs across broad areas, local-scale variability in environmental conditions can lead to heterogeneity in the severity of bleaching and in post-bleaching survival and recovery (Brown, 1987; Fisher et al., 2019; Hoogenboom et al., 2017; Nakamura et al., 2005). Even on the most severely bleached reefs, some coral colonies resist, or recover from bleaching (Hoogenboom et al., 2017; Hughes et al., 2017; Hughes et al., 2019b). Variation in environmental conditions at local scales (within and between reefs within a geographical region) including tidal movements and wave action (DeCarlo & Harrison, 2019; Donovan et al., 2021; Green et al., 2019), water flow (Nakamura et al., 2005; Nakamura & van Woesik, 2001), turbidity (Fisher et al., 2019; Morgan et al., 2017; Sully & van Woesik, 2020), island-shading effects (Fabricius et al., 2004), and cloud cover (Mumby et al., 2001a; Mumby et al., 2001b; Skirving et al., 2017) have proven important in driving heterogeneity in bleaching severity and post-bleaching survival at these scales. Quantifying the role that these environmental factors play in driving survivorship and recovery post-bleaching can improve our capacity to predict future coral population trajectories (Donovan et al., 2021).

Variable bleaching responses can also be due to genetic variation within coral populations (Baird et al., 2009; Howells et al., 2013) and their obligate Symbiodiniaceae (sensu LaJeunesse et al., 2018) photosymbiont communities (Baker, 2003; Bay et al., 2016). Host sensitivity to heat stress, plasticity in heterotrophy, symbiont community composition, and symbiont shuffling can all contribute to within-population variation in bleaching (Abrego et al., 2008; Baker et al., 2008; Bay et al., 2016; Dixon et al., 2015; Grottoli & Palardy, 2006; Howells et al., 2013; Jones et al., 2008; Marangoni et al., 2019). How much of the variability in bleaching during any given heat wave is due to fine-scale environmental variation versus within-population genetic variation in corals or their photosymbionts is difficult to quantify. Differential survival of coral genotypes following bleaching and the increased occurrence of heat-tolerant *Symbiodinium* clades in surviving corals has also been shown to lead to the directional selection of more heat-tolerant and resilient locally adapted corals (Dixon et al., 2015; Howells et al., 2013; Sully et al., 2019), changing this balance over time.

Coral species also vary in their sensitivity to environmental conditions, including heat and light stress, and are therefore differentially susceptible to bleaching (Guest et al., 2012; Hoogenboom et al., 2017; Loya et al., 2001; Marshall & Baird, 2000; McClanahan, 2020; Swain et al., 2017). Many fast-growing branching genera (i.e., *Acropora*, *Pocillopora*, *Stylophora*, and *Seriatopora*) are often more likely to bleach and die than slower growing coral taxa (Loya et al., 2001; Marshall & Baird, 2000; McClanahan, 2020; Swain et al., 2017; van Woesik et al., 2011). These same branching coral taxa, particularly of the genus *Acropora*, are additionally vulnerable to other disturbances due to their propensity to fragment following storms and cyclones (Fabricius et al., 2008; Madin, 2005), high disease susceptibility (Patterson et al., 2002; Randall & van Woesik, 2015; Sutherland et al., 2004; Willis et al., 2004), and because they are the preferred prey of corallivores including *Drupella* and crown-of-thorns starfish (Forde, 1992; Pratchett, 2007). In a warmer world in which disease outbreaks, severe tropical cyclones, and regional-scale bleaching events are increasing in severity and frequency (Harrison et al., 2019; Harvell et al., 1999; Heron et al., 2016; Hughes et al., 2017; Ward & Lafferty, 2004; Webster et al., 2005), the ongoing persistence of these sensitive coral taxa is at risk (Côté & Darling, 2010). Certainly the susceptibility of Caribbean acroporids to disease, hurricanes, and bleaching has contributed to their endangered listing (Diaz-Soltera, 1999; Precht et al., 2002; Randall & van Woesik, 2015). Understanding how coral taxa differ in their susceptibility to disturbances is integral to predicting how coral communities may change in a warmer world (Côté & Darling, 2010).

Highly disturbed reefs provide an opportunity to investigate the potential impacts of climate change, both on coral populations and communities. The Keppel Islands, located in the southern inshore Great Barrier Reef (GBR), lie approximately 30 km from the mouth of the Fitzroy River, which drains the largest GBR catchment (Furnas, 2003). These rocky continental islands and outcrops, sited in a shallow sandy bay, experience a 4-m tidal range that generates strong currents and high turbidity (Furnas, 2003; van Woesik & Done, 1997; Water Technology, 2013). Reefs in this region are considered "highly disturbed" and have been impacted by six major flooding events, four cyclones, four major storms, and six coral-bleaching events driven by marine heat waves over the past 30 years (Figure 1) (Diaz-Pulido et al., 2009; Jones & Berkelmans, 2014; Thompson et al., 2021; van Woesik et al., 1995). Bleaching in 1998, 2002, and 2006 was severe (greater than 60% of coral cover bleaching) (Berkelmans et al., 2004; Diaz-Pulido et al., 2009), while bleaching in 2016 and 2017 was comparatively mild (Kennedy et al., 2018; Thompson et al., 2021). Despite frequent disturbances, coral communities in the Keppel Islands continue to be dominated by disturbance-sensitive branching *Acropora* species (Thompson et al., 2021). Rapid recovery of *Acropora* via asexual fragmentation and regrowth of remnant tissue, combined with rapid *Acropora* growth rates documented in this region (Diaz-Pulido et al., 2009), may, at least in part, explain the ability of *Acropora* colonies to rapidly recover from disturbances and maintain their dominance in this region (Diaz-Pulido et al., 2009; Thompson et al., 2021). Local adaptation to these disturbances is also supported by genetic data indicating that the Keppel Islands' *Acropora millepora* population receives little genetic input via sexual recruitment from other GBR populations (van Oppen et al., 2015). Self-seeding via sexual recruitment is also likely to contribute to reef recovery following disturbances; however, in recent years, recruitment of Acroporidae in the region has been historically low (Davidson et al., 2019).

Regional-scale bleaching events provide an opportunity to explore how spatial heterogeneity in environmental conditions, including water flow and heat stress, contribute to variation in bleaching and recovery and can improve our ability to predict how coral communities may fare in a warmer climate. In this study, we analyzed a bleaching event that impacted much of the GBR in early 2020 (Hughes & Pratchett, 2020), to (1) characterize the heat stress experienced across Keppel Island sites using remotely sensed and modeled seawater temperature and ocean current data, compared with a historical climatology, (2) track coral bleaching and survival among taxa and across depths at six reef sites, (3) quantify site-specific bleaching-induced mortality in *A. millepora*, and (4) investigate the role of heat stress and flow rate in driving bleaching and recovery. Results of this study provide insights into the current resilience of coral communities to heat exposure and bleaching in this highly disturbed region and highlight the likelihood of this region maintaining its current coral community composition in the near future.

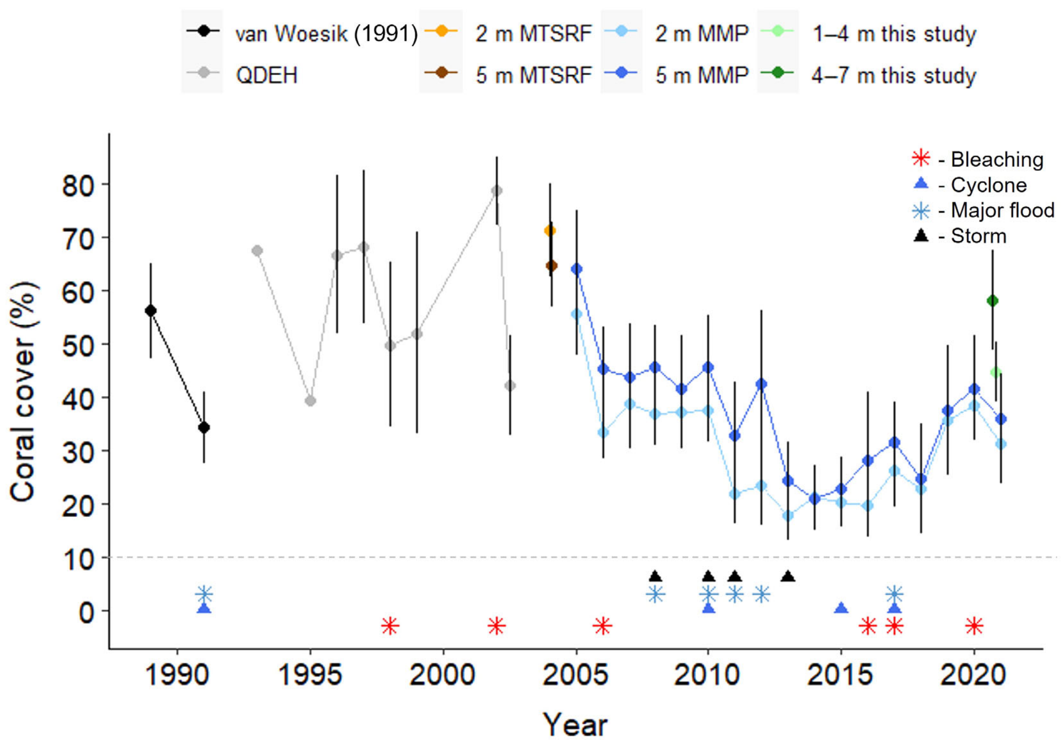

FIGURE 1 Historic cover of scleractinian corals in the Keppel Islands from 1989 to 2021. Disturbances: red asterisks = bleaching; black triangles = storms; blue triangles = cyclones; blue asterisks = floods. Data sources: black = van Woesik (1991); gray = Queensland Department of Environment and Heritage (QDEH) (unpublished data); orange (2 m) and brown (5 m) = Marine Tropical Sciences Research Facility (MTSRF) (Sweatman et al., 2007); light blue (2 m) and dark blue (5 m) = Great Barrier Reef Marine Park Authority Marine Monitoring Program (Thompson et al., 2021); light green (1–4 m) and dark green (4–7 m) = this study.

METHODS

Regional-scale climatology

To provide context for the thermal history of the Keppel Islands, long-term (150 years) mean monthly sea surface temperatures (SSTs) from January 1870 to January 2021 were obtained from the Met Office Hadley Centre reconstructed sea surface temperature (HadISST) record at a course-gridded $1 \times 1^{\circ}$ spatial resolution (Rayner, 2003). The data were obtained from a centrally located point within the grid cell that encompasses the greatest coverage of the Keppel Islands (23°30′0″ S, 151°30′0″ E). A climatological monthly mean (CMM) temperature was constructed from an 80-year reference window of 1870–1950 and monthly thermal anomalies (SST_A) from 1870 to 2021 were calculated as the difference between the monthly temperature (MT) and the CMM (Equation 1).

$$SST_A = MT - CMM \tag{1}$$

Trends in monthly SST, monthly SST_A, and annual SST minima and maxima were visualized in R (R Core Team, 2020) using the package "ggplot2" (Wickham, 2016). A linear model was used to evaluate the rate of change of each SST metric in base R (R Core Team, 2020). To examine the frequency of thermal anomalies in the Keppels, and to assess their temporal distribution over the last 150 years, the detrended and centered monthly SST_A record was deconstructed into time-frequency space using spectral analysis. A Morlet univariate wavelet transform model was generated using the "biwavelet" package (Gouhier et al., 2018) in R (R Core Team, 2020), and the frequencies were confirmed by evaluating spectral densities.

Site-specific climatology and degree heating week calculations

Daily modeled seawater temperature (in degrees Celsius) and eastward and northward current (in meters per second) data were extracted for each of the study sites from the GBR1 Hydro V2 eReefs model (Herzfeld et al., 2016; Schiller et al., 2015; Steven et al., 2019) for the entire available temporal range (1 December 2014 to 12 February 2021) using the online extraction tool (https://extraction.ereefs.aims.gov.au/) (CSIRO, 2021a, 2021b, 2021c). The GBR1 Hydro V2 eReefs model (hereafter GBR1) is described in detail in Schiller et al. (2015), Herzfeld et al. (2016), and Steven et al. (2019). Briefly, it is a comprehensive interoperable information platform that integrates data, catchment, and nested marine models to predict the physical state of the marine environment (Herzfeld et al., 2016; Schiller et al., 2015; Steven et al., 2019). GBR1, accessible via the eReefs platform (https://ereefs.aims.gov.au/ereefs-aims#ereefs-hydro-model), can be described concisely (in hydrodynamic modeling terms) as a three-dimensional, baroclinic hydrodynamic model that uses the Navier–Stokes equations for incompressible fluids. It uses a-coordinates in the vertical dimension and a curvilinear grid horizontally. Heat fluxes and water flow are calculated using well-established physical equations, driven by the Bureau of Meteorology's regional ACCESS meteorological data products (Herzfeld et al., 2016).

GBR1 uses a downscaling approach to represent the GBR domain at a 1-km resolution through a bridging 4-km model (GBR4 Hydro eReefs model) (Steven et al., 2019). The online extraction tool applies an inverse distance weighted interpolation from the nearest six neighbors to model the hydrodynamic data at a given site coordinate. A 4-year model calibration and validation against SST observations from the NOAA's Advanced Very High-Resolution Radiometer sensors on the NOAA Polar-orbiting Operational Environmental Satellites, via the Integrated Marine Observing System, indicated that the GBR1 performed better than the GBR4 (Herzfeld et al., 2016). The GBR1 model has been used recently to accurately hindcast a coral-bleaching event on the GBR, particularly for inshore reefs (Baird et al., 2018).

Modeled temperature and current data were extracted at a depth of 2.35 and 5.35 m for the shallow and deep sites, respectively. A climatological weekly mean (CWM) temperature for each site and depth was calculated from 2015 to 2019 and a modified degree heating week (mDHW) metric was calculated from 1 January to 31 April 2020 as the sum of the difference in the weekly maximum daily temperature (WMT) and the CWM temperature, when greater than 1, divided by 7 (Equation 2). The mDHW was used to characterize the level of heat exposure experienced by the corals at each site during the height of the heat wave. The mDHW calculation was chosen to allow us to use the limited data available (2015–2019) and represents a conservative estimate of heat exposure given the recent baselines used in these calculations.

$$mDHW = \text{if}(WMT - CWM > 1) \sum (WMT - CWM)/7 \tag{2}$$

To investigate the role of flow rate in bleaching and recovery, the absolute values for eastward and northward (in meters per second) currents were calculated for each site, to account for water flow in both positive (eastern or northern) and negative (western or southern) directions. Then, the median and maximum daily currents were averaged from January to June 2020, during the height of the thermal stress and recovery periods, for each of the northern/southern and eastern/western directions.

Field surveys of coral bleaching and benthic cover

To document the severity of coral bleaching during the 2020 marine heat wave, surveys were completed at six reefs in the Keppel Island region in early April 2020 following reports of widespread and severe bleaching (Appendix S1: Table S1; Figure 2). Survey sites were haphazardly selected and chosen with no prior knowledge of the severity of bleaching. Photo transect surveys were completed at both a shallower upper reef slope (~1–4 m below the lowest astronomical tide [LAT]) and a deeper lower reef slope (4–7 m below LAT) site at each reef, except at Pumpkin Island and Shelving Bay (Great Keppel Island) where surveys were only completed on the shallow reef slope due to time constraints and the absence of a deep reef slope, respectively. Surveys were repeated at these and an additional three sites in June and October 2020 (also selected haphazardly

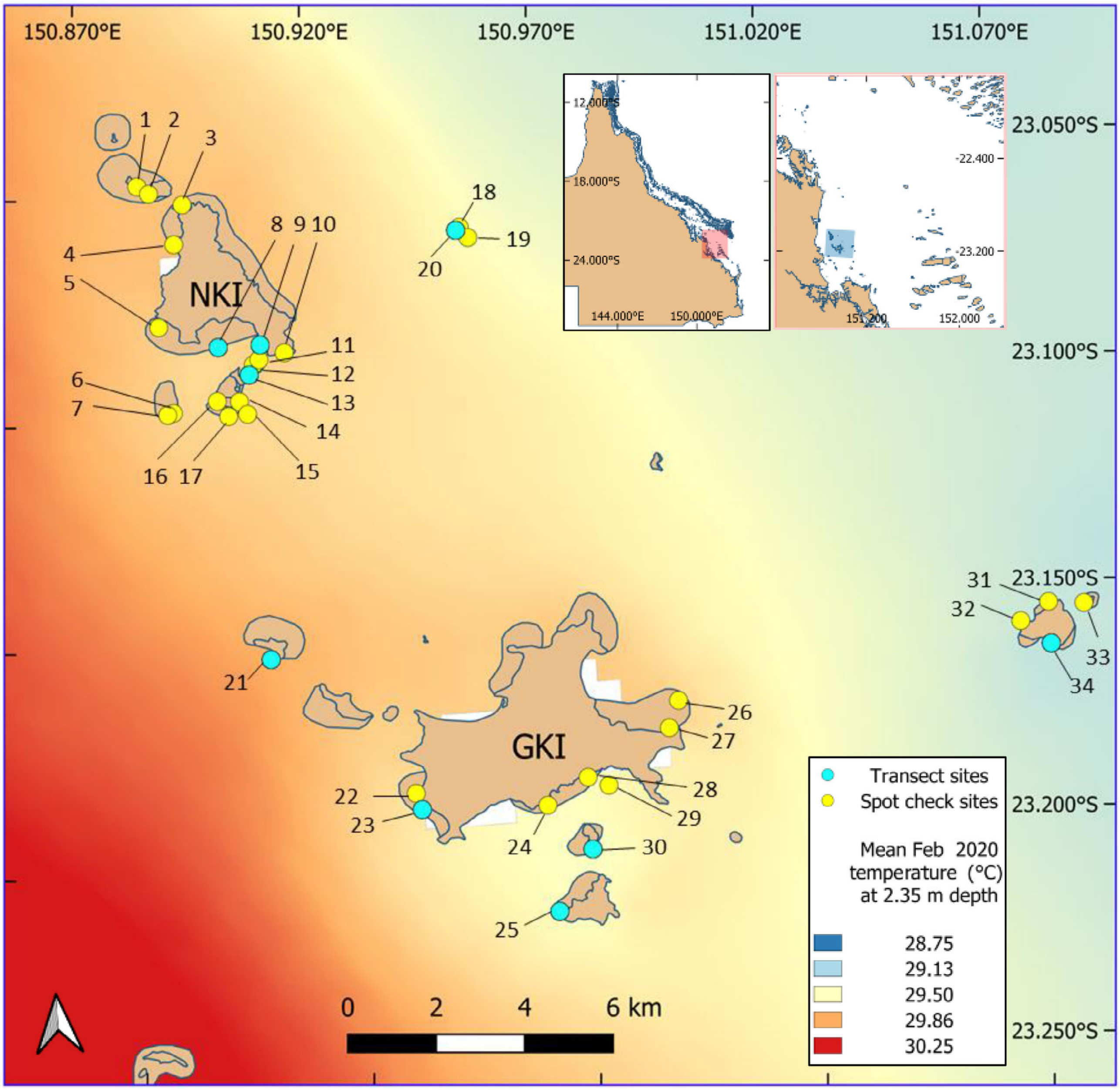

FIGURE 2 Map of the Keppel Islands region with field sites identified. Site numbers and site name abbreviations are defined in Appendix S1: Table S1. Map background color represents the mean temperature in February 2020 at the height of the heat wave, at 2.35 m depth, as modeled by eReefs (www.ereefs.aims.gov.au).

to represent a larger number of reefs; Figure 2) to document the impact of, and recovery from, bleaching among sites and taxa (Appendix S1: Table S1). Photo transect and photo sampling methods closely followed those used by the Australian Institute of Marine Science (AIMS) Long-term Monitoring Program (Jonker et al., 2008) and are briefly outlined below.

At each site, five 20-m transects were haphazardly laid along the deep and shallow reef slopes along the reef contour. The start of each transect was separated from the end of the previous transect by at least 5 m. On one side of the transect, a 34-cm-wide belt was photographed. Photos of the benthos were taken at 50-cm intervals, ensuring that photos did not overlap. The camera lens was held parallel to the reef substrate and the camera height above the substrate was maintained at approximately 1 m to ensure consistency in the surface area included in each photograph (approximately 850 cm^2/photograph). The number of photographs recorded per transect averaged 31 ± 10 (SD), equating to an average survey area of 132 m^2 per site per depth.

Photographic analyses

Estimates of the benthic community composition were derived from point-count analyses. Ten points were overlaid in an even distribution on each photograph and the benthic organism under each point was identified to the lowest possible taxonomic level, with most Scleractinia (stony corals), Alcyonacea (soft corals), and macroalgae identified to genus. For points identified as stony corals (hereafter "corals"), the level of bleaching was recorded as either not bleached, pale, or fully bleached, consistent with methods described in Jonker et al. (2008). Coral points scored as not bleached appeared normally pigmented and showed no signs of paling (corresponding to a score of 5 or 6 on the Coral Watch Coral Health Chart, although the Chart was not used to score points in this study; Siebeck et al., 2006). Corals scored as pale were fluorescent in color or lighter in color than normal for that taxon, but not bright white (corresponding to a score of 2–4 on the Coral Health Chart). Bleached corals appeared bright white, corresponding to a score of 1 on the Coral Health Chart. Since branch tips typically represent new growth and are consequently paler than the rest of the colony, points that fell on colony tips were scored based on pigmentation observed in adjacent parts of the colony. Alcyonaceans were examined for bleaching, but none showed any such signs and were thus excluded from the analysis.

To examine the spatial variation in bleaching more widely, spot checks were completed at an additional 25 haphazardly chosen sites in June 2020 (Appendix S1: Table S1). Photos of coral communities at these spot check locations were haphazardly taken on snorkel. Images were taken parallel to the reef benthos and from 1 to 3 m above the benthos. For each site, the benthic composition and bleaching severity and prevalence were determined from 10 photos randomly chosen from those taken at each location, as described above for photo transects (Jonker et al., 2008). Scleractinian points scored as bleached and pale were pooled and collectively referred to as "bleached" in all statistical analyses.

Statistical analyses of bleaching

Temporal trends in bleaching were investigated by modeling the total numbers of bleached and unbleached scleractinian points per photograph per transect against survey month and depth and their interaction (fixed factors) using a generalized linear mixed effects model (GLMM) with transect nested in reef included as a random effect (random intercept) and using a beta-binomial distribution and a logit link function. Because time-series data were required for this analysis, only sites surveyed during all three periods were included ($n = 10$; Appendix S1: Table S1). Models were run using the "glmmTMB" package (Brooks et al., 2017). Model assumptions including homogenous variance and normally distributed residuals were verified using the "DHARMa" package (Hartig, 2021). For significant models, pairwise comparisons were undertaken by calculating least squares mean with a Tukey adjustment using the "emmeans" package (Lenth, 2021).

Differential susceptibility to bleaching across coral genera was investigated by modeling the total numbers of points scored as bleached or not bleached per photograph at the height of bleaching in April 2020 against genus (fixed factor) using a GLMM. We note that points in these data do not necessarily represent individual coral colonies. Replicate transects nested in depth, within reef, was included as a random effect (random intercept). Data were modeled using a binomial distribution and a logit link function. Only those genera representing at least an average of 5% of coral cover across transects (*Acropora*, *Pocillopora*, *Montipora*, and *Porites*) could be included in this analysis due to data limitation. *Pocillopora* was subsequently excluded due to issues with model convergence given the high proportion of points bleached in this genus. Model assumptions of homogeneity of variances and normally distributed residuals were verified using the package "DHARMa" (Hartig, 2021). Only sites surveyed during the height of the bleaching (April 2020) were included in this analysis ($n = 10$; Appendix S1: Table S1).

To determine whether differential taxonomic susceptibility to bleaching was consistent across depths, the total numbers of points scored as bleached and not bleached per photograph were modeled against the interaction between genus and depth (fixed factor) using a GLMM. Transect nested in reef nested in depth was included as a random effect in this model with a beta-binomial distribution and logit link function. Only the genera *Acropora* and *Montipora* were included in this model as these were the only genera for which sufficient data were available from both depths. Model assumptions were verified and post hoc pairwise comparisons were completed as described above.

Again, only sites surveyed during the height of the bleaching (April 2020) were included in this analysis ($n = 10$; Appendix S1: Table S1).

A GLMM was also fitted to investigate whether the cover of scleractinian corals declined over the 6 months following bleaching. Survey month and depth and their interaction were included as fixed factors and transects nested in reef were included as a random factor, to account for variation among reefs. Scleractinian and non-scleractinian points per photo per transect were modeled with a beta-binomial distribution and logit link function, as described above. All statistical analyses were completed in R (R Core Team, 2020) and data visualizations were completed using the R package "ggplot2" (Wickham, 2016). Because time-series data were required for this analysis, only sites surveyed during all three periods were included ($n = 10$; Appendix S1: Table S1).

Fate-tracked colonies

To substantiate the results from the survey sites, estimates of whole-colony mortality following bleaching were determined from *A. millepora* colonies that were fate-tracked at four reefs during the bleaching event (18–21 April 2020) and resurveyed in October 2020. Adult colonies (9.5–73 cm in diameter, average diameter = 30 cm) were haphazardly chosen to represent the range of colony responses to heat stress (from severely bleached to non-bleached), although given the severity of bleaching in the region, few colonies (~11% colonies) remained unbleached. Approximately 100 colonies were tagged on the shallow reef flat (~1–2 m below LAT) at each of Pumpkin Island, North Keppel Island, and Halfway Island, while 50 colonies were tagged at Great Keppel Island, for a total of 350 tagged colonies. Colonies were located upslope of photo transect sites at these same locations, as that is the primary habitat of *A. millepora* in the Keppels. In October 2020, colonies that could be found were resurveyed and recorded as dead or alive.

Relationships between bleaching recovery and environmental variables

The relationships between environmental conditions (heat and flow metrics) and both bleaching (in April 2020) and recovery from bleaching (between April and June 2020) were examined by modeling the maximum daily temperature during the 2020 heat wave, the mDHW values, and the average flow rates against (1) bleached *Acropora* cover, and (2) the change in the proportion of bleached *Acropora* cover between April and July across the photo transect sites that were surveyed in both months ($n = 5$ reefs at each of two depths). To explore the relationships between the environmental conditions (heat and flow) that persisted through to June 2020 and bleaching, the same environmental metrics were modeled against the proportion of *Acropora* cover bleached in June across all transect and spot check sites ($n = 42$). The model was also run to include photo transect sites only for the June 2020 data. Because the sites were clustered in space (Figure 2), a Moran's *I* test for distance-based autocorrelation was calculated for each model using the DHARMa package (Hartig, 2021), and where spatial autocorrelation was significant (at $p < 0.05$), a spatial dependence correlation structure was applied to the models. The structures tested included an exponential, a Gaussian, a rational quadratic, and a spherical structure, and the best model was selected based on the lowest Akaike information criteria (AIC) estimates and verified using a semivariogram. Models were run using the "gls" function from the R package "nlme" package (Pinheiro et al., 2014). Only *Acropora* cover was used in this analysis given the dominance of this genera in this region (comprised ~82% of coral cover per site) and to remove the influence of site-level variation in coral community composition and the differential susceptibility of coral taxa to bleaching from this analysis. The data, as described above, were modeled with a linear model using generalized least squares fit by restricted maximum likelihood. Data and R code are publicly available at AIMS (2022).

RESULTS

Long-term temporal trends in heat stress in the Keppel Island region

Average SSTs in the Keppel Islands have increased 0.8°C over the past 150 years (Figure 3a,b). The rate and frequency of anomalously warm months is also increasing, with evidence of significant frequent (1–4 years) anomalies since about the 1970s (Figure 3c). The increase in average temperatures is driven by increases in both annual temperature minima and maxima (Figure 3a), with annual minima

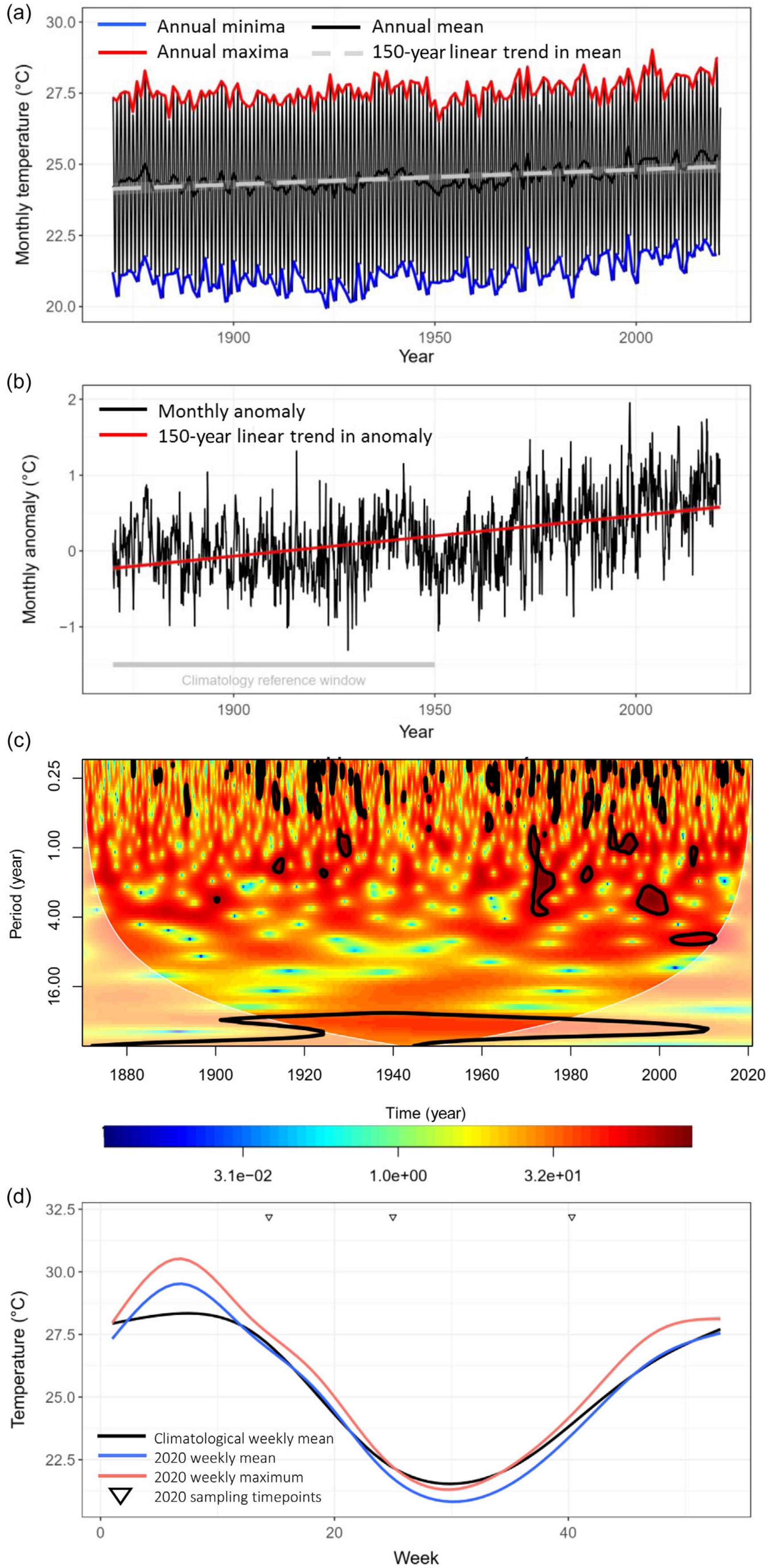

FIGURE 3 Legend on next page.

increasing at a faster rate (0.9°C 150 years^{-1}) than annual maxima (0.7°C 150 years^{-1}). Since February 2014, 90% of the MT anomalies in the Keppel Islands have been warmer than the climatological average (Figure 3b).

During the 2020 marine heat wave, average weekly seawater temperatures in the Keppel Islands started to exceed the recent (2015–2019) climatological mean temperature (CMT) in mid-January 2020 and continued to exceed the CMT for 8 weeks until mid-March (Figure 3d). Maximum water temperatures in the Keppel Islands rose sharply and peaked in mid-February at 32.0°C at Miall Island, 3.5°C above the climatological mean (Figure 3d). Cumulative heat stress, measured as mDHWs from 1 January to 31 April 2020, ranged between 3.75 and 7.95 and was highest inshore of the northern islands group (North Keppel, Conical, Corroboree, Pumpkin, and Sloping Islands and Square Rocks) as well as inshore of Miall Island, which lies to the north of the southern island group (Figure 2). Cumulative heat stress was lowest at the offshore sites: Barren Island, The Child, Bald, and Outer Rocks (Figure 2). Maximum daily seawater temperatures between 1 January and 31 April 2020 varied between 26.1 and 32.0°C. The summer/autumn 2020 marine heat wave was followed by a cooler-than-average winter/spring in the Keppel Islands, relative to the recent climatology (2015–2020). Water temperatures were cooler than the climatological mean by as much as 1.2°C (Figure 3d).

Patterns in bleaching severity in April 2020

In early April 2020, coral bleaching was widespread and severe at all sites surveyed (Figures 4 and 5) and at other sites throughout the Keppel Islands from which reports of bleaching were available (Hughes & Pratchett, 2020; North Keppel Island Environmental Education Centre, 2020). Surveys revealed that more than 75% of live coral was bleached at all sites, with ≥90% of live coral cover bleached at 7 of the 10 sites (Figure 5). Bleaching was most prevalent on the shallow reef at Barren Island (98.5%) and lowest on the shallow reef at Halfway Island (75%) (Figure 5). Very recent coral mortality, evident as bright white coral skeleton denude of coral tissue and fouling organisms, was recorded from all sites but represented less than 3% cover. No bleaching was recorded in any other taxonomic group (i.e., soft corals, anemones, and clams), although these taxa are not common on the reefs surveyed. The prevalence of bleaching did not differ between deep (4–7 m) and shallow reefs (1–4 m) (pairwise comparison: $p = 0.97$; Figure 6a). On average 92.3 ± 1.2% of coral cover was bleached at deep sites compared with 89.7 ± 1.7% at shallow sites (Figure 6a).

Repeat surveys of those sites surveyed in April 2020, combined with additional sites surveyed using photo transect and spot check methods, revealed the persistence of bleaching in June at all but one site (East Clam Bay, GKI). Recovery was more rapid at deep sites compared with the shallow sites (GLMM: deep—June 2020: $z = -3.55$, $p \leq 0.001$; Table 1) and by June 2020, the proportion of corals bleached was lower at deep sites (23.8 ± 2.3% cover) than at shallow depths (35.6 ± 2.9% cover; pairwise comparison: $p < 0.0001$; Figure 6a). By October 2020, bleached corals were rare and occurred at only the shallow reef at Halfway Island. Pale corals were recorded at all sites, but these generally constituted less than 10% of coral cover (Figure 5). The proportion of coral cover bleached was similarly low at both shallow (3.4 ± 1% cover) and deep sites (0.19 ± 0.6% cover pairwise comparison: $p = 0.34$; Figure 6a).

Impact of bleaching on coral survival and cover

Despite the severity of bleaching, survival of *A. millepora* colonies was high (Figure 7). No whole-colony mortality occurred at North Keppel Island, while whole-colony morality was highest at Pumpkin Island (17% of colonies) (Figure 7). Consistent with these results, average cover of corals in October 2020, six months after bleaching, did not differ from that initially recorded in April 2020 at both shallow and deep sites (shallow sites: April cover = 50.4 ± 2.5%, October cover = 49.7 ± 1.9%, pairwise comparison: $p = 0.97$; deep sites: April cover = 62.3 ± 2%, October cover = 65.5 ± 2.5%, pairwise comparisons: $p = 0.97$) (Figure 6b, Table 2).

Differential susceptibility of scleractinian taxa

Keppel Island coral communities were dominated by the genus *Acropora*, particularly the branching species

FIGURE 3 (a) Monthly sea surface temperatures in the Keppel Islands from 1870 to 2020 with annual maxima and minima. Mean and 150-year trend lines are overlaid. (b) Monthly sea surface temperature anomalies in the Keppel Islands from 1870 to 2020, with the linear trend overlaid, and the reference window for anomaly calculations identified. (c) Morlet wavelet model output indicating the periodicity of sea surface temperature anomalies in the Keppel Islands from 1870 to 2020 (from (b)). Color bar represents the power spectrum, indicating the strength of the signal in time-frequency space. All regions within black contour lines represent 95% confidence limits of statistically significant periodicities ($p \leq 0.05$). The white line indicates the "cone of influence" and periodicities identified outside this region (shaded area) should be approached cautiously. (d) The weekly recent climatological mean, with the 2020 weekly mean and maximum overlaid for the Keppel Islands.

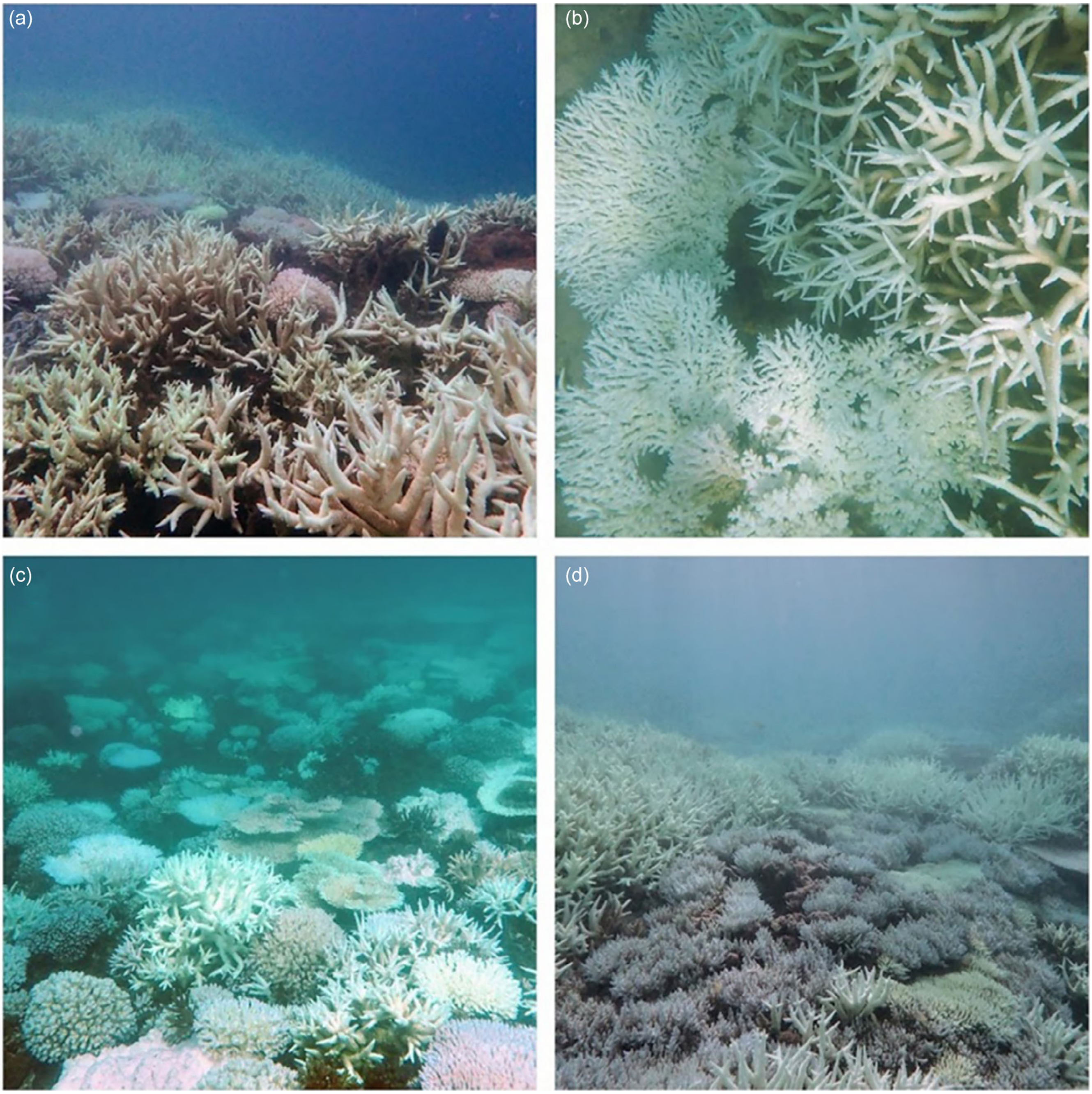

FIGURE 4 Examples of bleached corals in April 2020, at (a) Outer Rock, (b) Mazie Bay, North Keppel Island, (c) Halfway Island, and (d) Barren Island. Photo credits: (a) and (b) D. Brighton and (c) and (d) S. Gardner.

A. muricata and *A. intermedia*. In April 2020, *Acropora* corals comprised 82 ± 6.8% of points sampled and on average 48.5 ± 6% of benthic cover per site. (Figure 8a). Only three other coral genera, *Pocillopora*, *Porites*, and *Montipora*, were present at greater than an average of 5% cover per transect (Figure 8a). These common coral taxa were also the most susceptible to bleaching (Figure 8b), with 96.6 ± 3.4% of *Pocillopora* cover recorded as bleached. An average of 94.6 ± 0.9% of *Acropora*, 66 ± 12.9% of *Porites*, and 43.6 ± 5.8% of *Montipora* points sampled recorded as bleached (Figure 8b). *Acropora* points were as likely to be bleached as *Porites* points (pairwise comparison: $p = 0.105$; Table 3) and both *Acropora* and *Porites* points were more susceptible to bleaching than *Montipora* points (pairwise comparison: $p < 0.001$; Table 3). The susceptibility of the two most common coral genera, *Acropora* and *Montipora*, did not vary between depths, with *Acropora* points being more likely to be bleached than *Montipora* points at both depths (pairwise comparison: $p = 0.001$; Table 4).

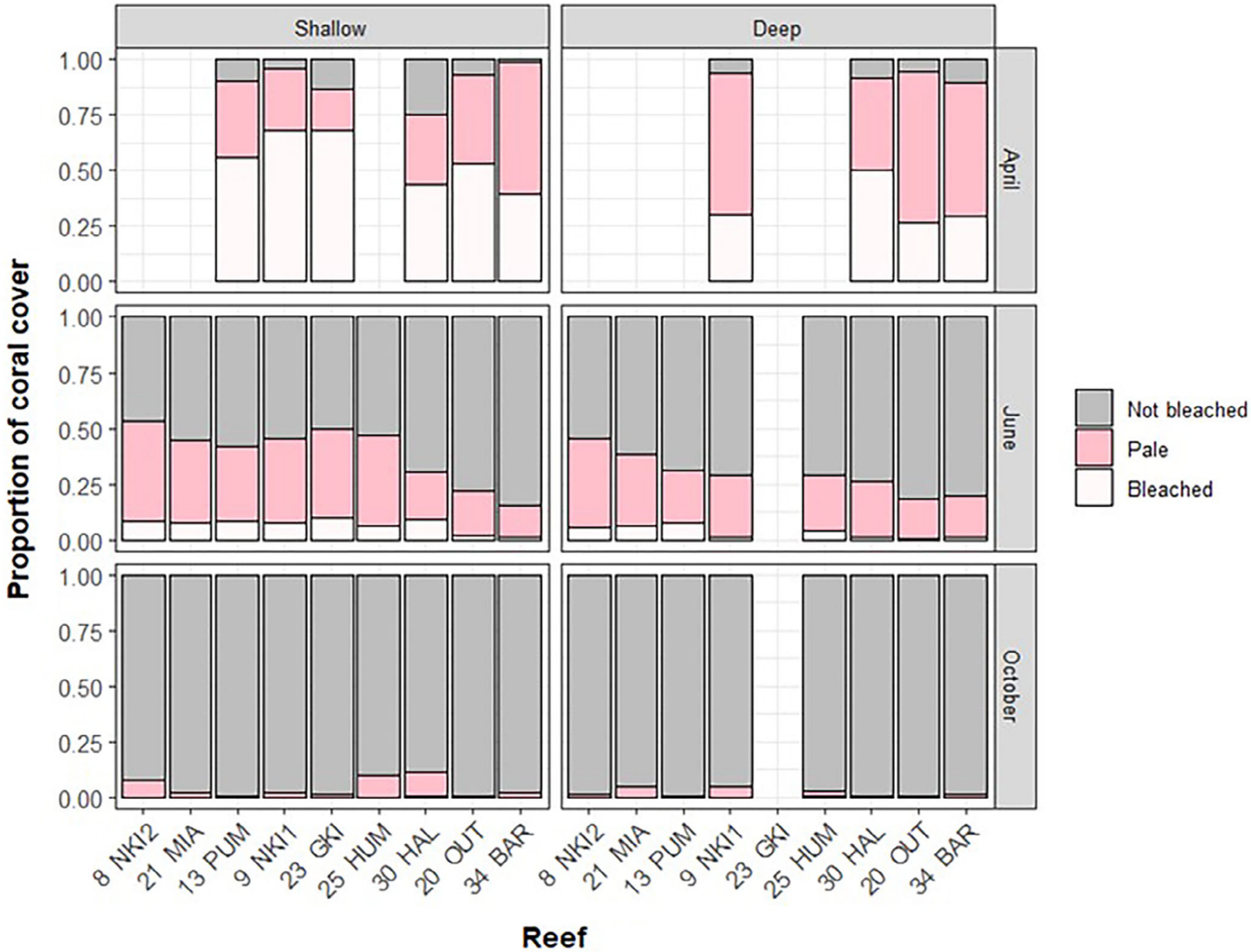

FIGURE 5 Proportion of coral cover bright white (bleached), pale, or normal in pigmentation (not bleached) at photo transect sites in April, June, and October 2020. Site numbers and site name abbreviations are defined in Appendix S1: Table S1. Site numbers are included in Figure 2 for cross-referencing.

Relationship between environmental metrics and recovery from bleaching

Bleaching severity in April 2020 did not correspond with metrics of heat exposure or flow rates, likely due to high bleaching (75%–98%) at all sites as a consequence of exceeding heat-exposure thresholds (Figures 2 and 9). All sites, including both shallow and deep reefs, experienced four or more degree heating weeks and at least a maximum daily temperature of 29.5°C from January to April 2020. The persistence of bleaching in June, however, was driven by accumulated heat exposure, and for every additional mDHW of exposure, an additional approximately 10% of corals remained bleached (Figure 9; Appendix S1: Tables S2 and S3). Similarly, for every 1°C increase in the maximum daily temperature experienced, an additional approximately 30% of corals remained bleached (Figure 9; Appendix S1: Table S2). Heat exposure in the lead up to bleaching was, therefore, a strong predictor of persistent bleaching in June 2020. Recovery from bleaching was slower at nearshore reefs where heat exposure was highest. Persistent bleaching in June 2020 was also often higher at shallow sites compared with deep sites having experienced the same exposure to accumulated heat (Figure 9). The exclusion of spot check sites from this model did not change the significance of these results (Appendix S1: Tables S2 and S3).

Neither bleaching severity in April and June, nor the recovery from bleaching, was significantly predicted by median flow rates, despite a tendency toward higher recovery and lower bleaching at higher flow sites. Flow rates were significantly correlated with cumulative mDHW or maximum daily temperatures, and higher heat exposure was recorded at sites with lower east–west flow rates (cumulative mDHW-median flow east–west: $F = 21.03$, $p < 0.001$, $r^2 = 0.328$) and higher maximum temperatures where rates of northerly water flow were highest (maximum daily temperature-median flow north–south $= 5.745$, $p = 0.023$, $r^2 = 0.10$; Appendix S1: Figure S2).

DISCUSSION

During early 2020, over 90% of shallow-water corals in the Keppel Islands bleached (Figure 5). This represents a much higher severity of bleaching than that recorded offshore at One Tree Island (~47% of coral cover) two months earlier (Nolan et al., 2021). This difference in bleaching severity likely reflects higher overall temperatures recorded at the Keppel Islands (>30°C compared with <30°C at One Tree Island) and potentially greater accumulation of heat exposure over the following two months at the Keppel Islands. The severity of bleaching in the dominant *Acropora* genus was high across sites, reflecting substantial heat stress across the entire region and therefore did not correlate with site-specific heat-stress metrics, in contrast to many historic studies (Berkelmans, 2001; Donovan et al., 2021; Glynn, 1993; Harrison et al., 2019; Heron et al., 2016; Hughes et al., 2017; Hughes et al., 2019b). These results add to the growing evidence that coral-bleaching thresholds are being exceeded across entire regions during marine heat waves and emphasize the decoupling of bleaching thresholds and bleaching severity. Although bleaching was severe across all sites surveyed in April 2020, our power to detect relationships between bleaching and environmental metrics was lower in April than in June due to our limited sample size. It is possible, therefore, that subtle effects of environmental conditions on bleaching in April went undetected. The occurrence of more frequent and severe marine heat waves under projected climate warming scenarios (Cai et al., 2014; Hoegh-Guldberg, 1999; Hughes et al., 2017; Timmermann et al., 1999), coupled with the accumulation of latent impacts of heat stress over multiple years, is likely to lead to a further decoupling of bleaching severity and the heat stress metrics that are currently in use (Hughes et al., 2019b; McClanahan et al., 2019; Neal et al., 2017). Metrics incorporating the accumulation of heat stress over multiple summers and accounting for the magnitude of winter reprieves or cooler than average conditions, overlaid on background rates of temperature rise, are likely to be more useful in predicting bleaching severity in the future (Hughes et al., 2017; McClanahan et al., 2019; Sully et al., 2019).

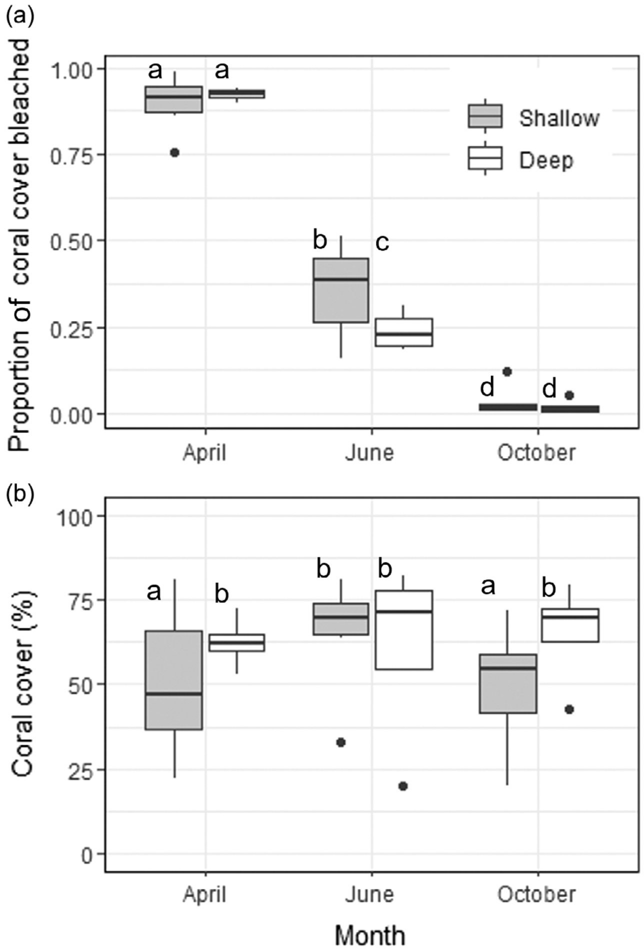

FIGURE 6 Temporal trends in (a) the proportion of corals bleached and (b) the percentage cover of scleractinian corals at Keppel Island reefs in April, June, and October 2020, across two survey depths. Lowercase letters indicate differences between groups based on Tukey's honestly significant difference (HSD) post hoc tests.

TABLE 1 Generalized linear mixed effects model summary statistics predicting the probability of a coral being bleached based on sampling month and depth.

Fixed effects	Estimate	SE	z	Pr(>|z|)
Intercept (April 2020—shallow)	2.4166	0.1674	14.43	**<2e−16**
June 2020	−3.0133	0.1045	−28.82	**<2e−16**
October 2020	−6.1571	0.1532	−40.19	**<2e−16**
Deep	0.1016	0.1338	0.76	0.447463
Deep—June 2020	−0.5418	0.1525	−3.55	**0.000381**
Deep—October 2020	−0.2702	0.2274	−1.19	0.234870

Note: Significant p values are indicated in boldface.

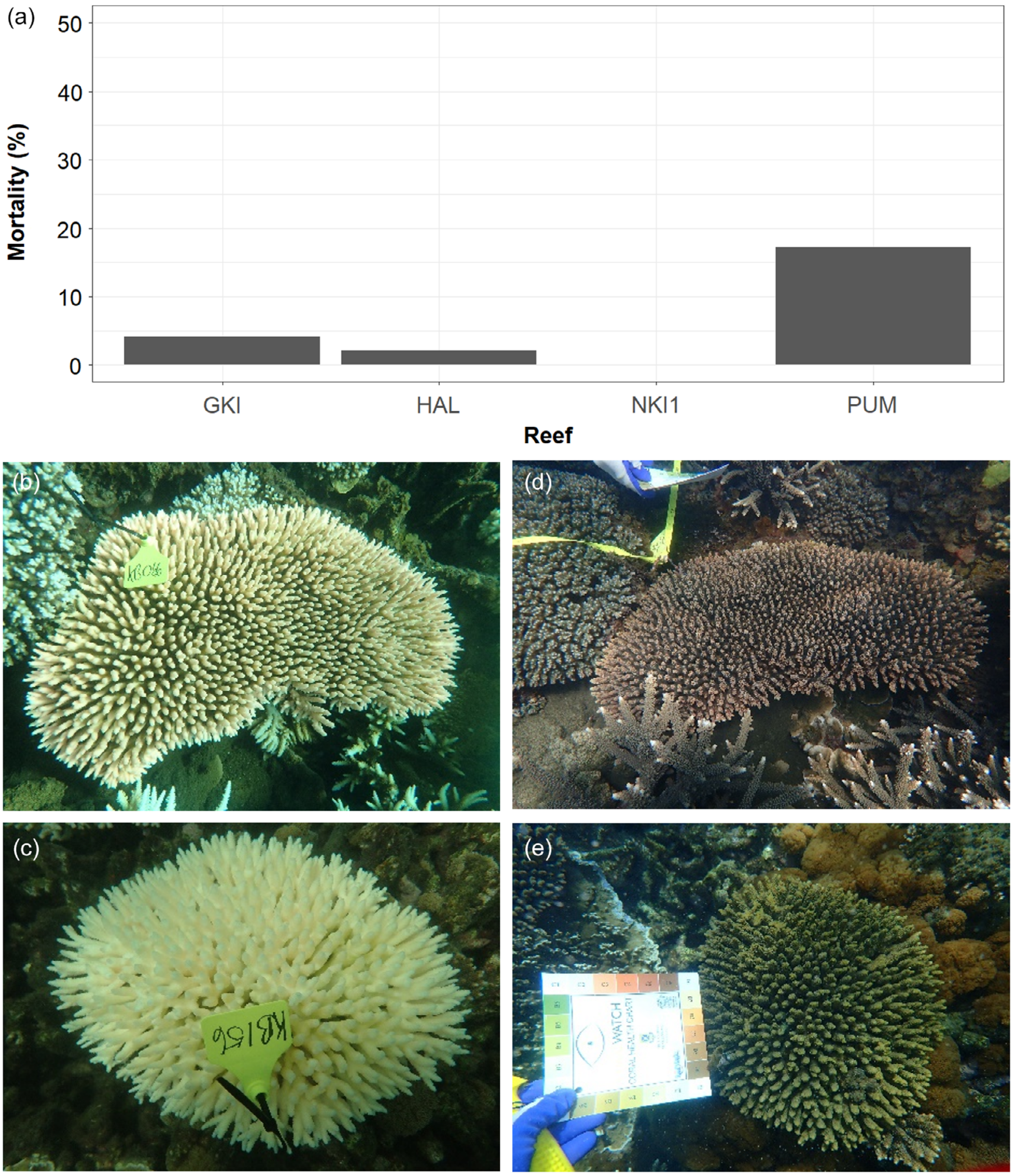

FIGURE 7 (a) Mortality of fate-tracked colonies of *Acropora millepora* at four sites in the Keppel Islands between April and October 2020. Photos demonstrate examples of bleached colonies in April (b and c) that had recovered by October 2020 (d and e). Photo credits: (b) and (c) D. Brighton and (d) and (e) C. Randall.

TABLE 2 Generalized linear mixed effects model summary statistics predicting the proportional cover of scleractinian corals based on sampling month and depth.

Fixed effects	Estimate	SE	z	Pr(>|z|)
Intercept (April 2020—deep)	0.7901	0.2378	3.322	**0.0009**
Shallow	−0.7940	0.0794	−10.003	**<2e−16**
June 2020	−0.1497	0.0783	−1.913	0.0558
October 2020	0.0508	0.0742	0.685	0.4936
June 2020—shall	0.8020	0.1042	7.701	**1.35e−14**
October 2020—shallow	−0.0996	0.0982	−1.015	0.3101

Note: Significant p values are indicated in boldface.

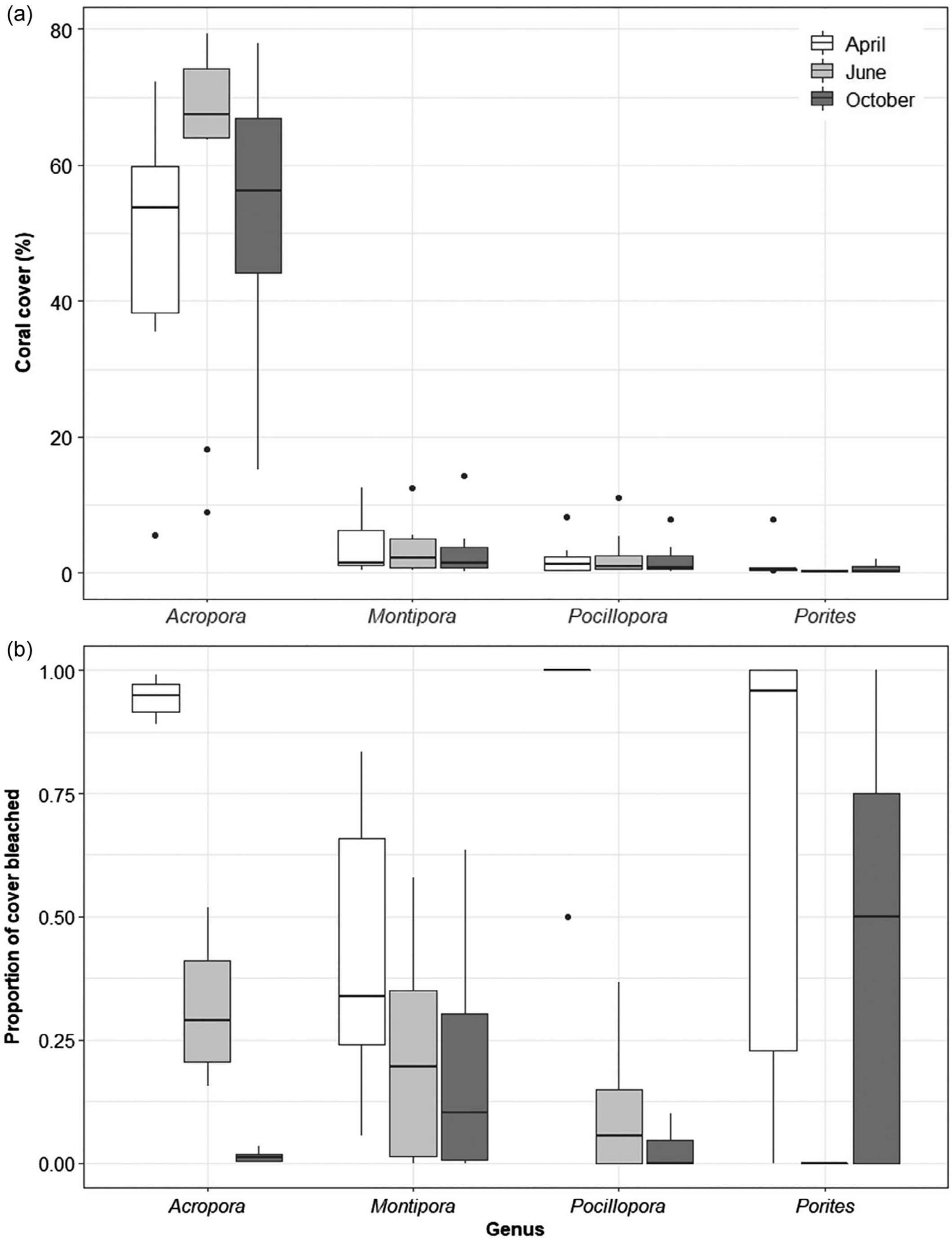

FIGURE 8 (a) Average cover (in percentage) of scleractinian coral genera per Keppel Island reef, and (b) the average proportion of cover scored as bleached per reef, in April, June, and October 2020. Averages are calculated from site-level averages. Error bars represent standard errors.

TABLE 3 Generalized linear mixed effects model summary statistics predicting the probability of a coral being bleached based on its taxonomic identity (*Acropora*, *Montipora* and *Porites* only).

Fixed effects	Estimate	SE	*z*	Pr(>|*z*|)
Intercept (*Acropora*)	3.7525	0.2776	13.519	**<2e−16**
Montipora	−4.0483	0.2657	−15.234	**<2e−16**
Porites	−0.3270	0.5002	−0.654	0.513

Note: Significant *p* values are indicated in boldface.

TABLE 4 Generalized linear mixed effects model summary statistics predicting the probability of a coral being bleached based on its taxonomic identity and depth (*Acropora* and *Montipora* only).

Fixed effects	Estimate	SE	z	Pr(>|z|)
Intercept (*Acropora*—deep)	2.4047	0.3044	7.900	**2.79e−15**
Montipora	−3.2418	0.3096	−10.470	**<2e−16**
Shallow	1.0106	0.2344	4.342	**1.63e−05**
Montipora—shallow	−0.4653	0.3831	−1.214	0.225

Note: Significant *p* values are indicated in boldface.

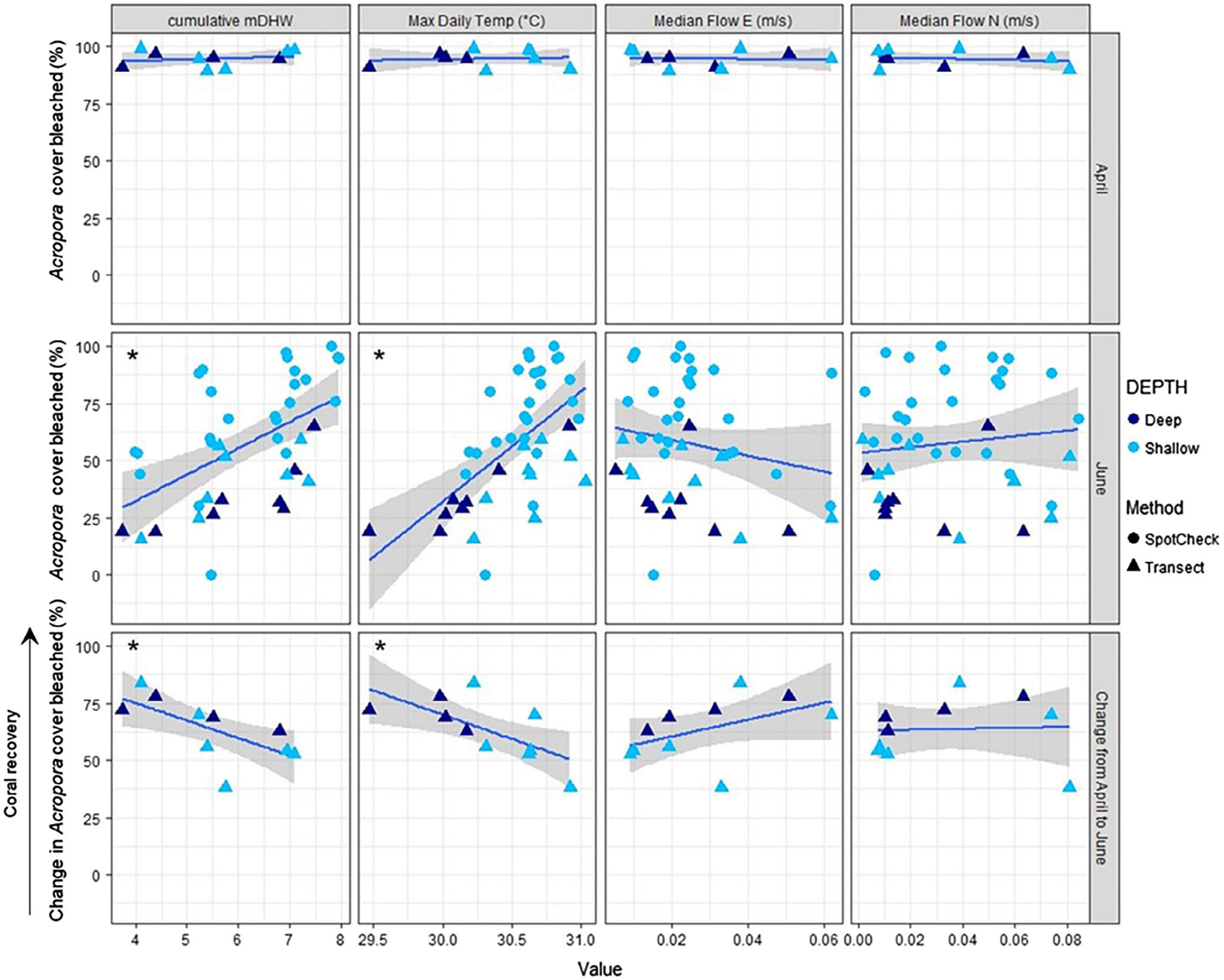

FIGURE 9 Relationships between the proportion of *Acropora* corals bleached in April and June 2020 (top and middle rows, respectively) and a suite of environmental metrics (columns; cumulative modified degree heating weeks [mDHW], maximum daily temperature [Temp.], and median flow rates in east–west and north–south directions). The bottom row indicates the relationship between the change in bleaching from April to June, as a proxy for recovery, and the environmental metrics (columns). Asterisks indicate statistically significant trends (Appendix S1: Table S1) and gray shading represents the 95% CIs around the models.

Severe bleaching events often result in high coral mortality (Brown, 1987; Glynn et al., 1998; Hughes et al., 2019a; Riegl, 2002; Stuart-Smith et al., 2018). Keppel Island corals, however, exhibited high survival and stable coral cover following bleaching in early 2020 (Figures 6b and 7; Thompson et al., 2021). Yet, recovery of bleached colonies was faster on reefs with lower heat exposure. For every additional mDHW of exposure, approximately 10%

more corals remained bleached in June 2020. Similarly, for every 1°C increase in the maximum daily temperature experienced, approximately 30% more corals remained bleached in June 2020 (Figure 9). High recovery across the region also may have been facilitated by cooler-than-average autumn and winter temperatures (Figure 3d). Nonetheless, the results of this study indicate that even where temperatures exceed bleaching thresholds, small differences in heat exposure can affect recovery trajectories in the months following bleaching. Therefore, while the magnitude of heat exposure may be becoming less predictive of bleaching severity, it may remain useful for predicting recovery rates following future bleaching events. Severity of bleaching and short-term mortality remain the focus of many coral-bleaching studies (Berkelmans et al., 2004; Harrison et al., 2019; Hughes et al., 2017; Mumby et al., 2001a; Mumby et al., 2001b). Results of this and other recent studies (Donovan et al., 2021; Stuart-Smith et al., 2018) highlight the importance of documenting coral survival or mortality over longer time frames in order to improve our understanding of the contribution of environmental variables to heterogeneity in coral survival and the impacts of bleaching on coral community composition.

High water flow can also reduce bleaching and/or accelerate recovery, and the Keppel region is characterized by a large tidal range and strong currents (Furnas, 2003; Thompson et al., 2021; van Woesik & Done, 1997). High flow can rid corals of superoxide radicals through passive diffusion (Nakamura et al., 2005; Nakamura & van Woesik, 2001) and can increase water mixing to reduce temperatures. Water flow in this and other inshore regions is also typically correlated with the resuspension of particulate organic matter (Kleypas & Hopley, 1992), on which inshore corals are adept at feeding (Anthony, 2000). Heterotrophy can provide an important source of nutrition for corals in the absence of their symbiotic Symbiodiniaceae populations and increase coral survival following bleaching (Grottoli & Palardy, 2006). Lower heat stress at sites with higher water flow in an east–west direction identified in this study likely reflects greater mixing of deeper, cooler offshore waters with warmer shallower inshore waters (Appendix S1: Figure S2). By contrast, high flow rates in a north–south direction drove high temperature stress, most likely because north–south water flow resulted in the mixing of waters of similar depths, and the transport of warm water northward from the shallow Keppel Bay. High rates of water flow and increased heterotrophy by inshore corals are likely to be important drivers of the high tolerance of Keppel corals to bleaching. Finally, irradiance stress exacerbates bleaching (Downs et al., 2013; Lesser et al., 1990), and high turbidity can reduce this by reflecting light and shading corals (Cacciapaglia & van Woesik, 2016; Fisher et al., 2019; Morgan et al., 2017; Sully & Woesik, 2020). Bleaching severity can be lower on turbid inshore reefs, such as the Keppel Islands, which may provide corals some protection from the effects of climate warming (Cacciapaglia & van Woesik, 2016; Fisher et al., 2019; Morgan et al., 2017; Sully & Woesik, 2020).

Consistent with previous studies, *Pocillopora* and *Acropora* were among the most susceptible genera to bleaching during the 2020 marine heat wave (Guest et al., 2012; Loya et al., 2001; Marshall & Baird, 2000; McClanahan et al., 2004) (Figure 8b). Interestingly, *Porites* corals were found to be moderately susceptible to bleaching, in contrast to previous studies that suggest that *Porites* corals are generally resistant to bleaching (Marshall & Baird, 2000; McClanahan et al., 2004). However, most *Porites* colonies sampled in this study were small sub-massive corals (possibly *Porites annae*), rather than the massive species of *Porites* that are often found to be resistant to bleaching (i.e., *Porites lobata*; Marshall & Baird, 2000). These sub-massive *Porites* colonies were often located in shallower habitats than those typically occupied by massive *Porites* colonies, which may, at least partly, explain their sensitivity to bleaching. Resistance to bleaching in *Porites* is however not universal (Guest et al., 2012; McClanahan, 2020; Mumby et al., 2001a; Mumby et al., 2001b), and differential taxonomic susceptibility has proven to be temporally and spatially variable both within and among reef regions (Guest et al., 2012; Hughes et al., 2017; Marshall & Baird, 2000; McClanahan, 2020; McClanahan et al., 2004). Sensitivity to bleaching does not always translate to high mortality (i.e., Figure 6b) and both rates of mortality and sublethal impacts of bleaching are likely to be species-specific (Baird & Marshall, 2002; Cox, 2007; Johnston et al., 2020; Muir et al., 2017; Szmant & Gassman, 1990). Taken together, this highlights the need to document species-specific bleaching, mortality and sublethal responses, to provide a more comprehensive understanding of the impacts of bleaching on coral communities' resilience (Côté & Darling, 2010; van Woesik et al., 2011).

The differential susceptibility of coral taxa to disturbance-mediated mortality can drive changes in the composition of coral communities (Aronson et al., 2002; Hughes, 1994; Johns et al., 2014; Loya et al., 2001; McClanahan, 2020; Pandolfi & Jackson, 2006), which may influence their vulnerability to future disturbances including bleaching (McClanahan, 2020). The dominant *Acropora* corals in the Keppel Islands were highly susceptible to bleaching yet survived (Figures 7 and 8a), indicating high resilience. The persistent dominance of *Acropora* over at least the past 30 years in this region, despite the occurrence of four cyclones, six bleaching events, and six storms (Figure 1), to which the *Acropora* corals are highly sensitive (Fabricius et al., 2008; Loya et al., 2001; Madin, 2005; Marshall & Baird, 2000; van Woesik et al., 1995), supports this conclusion. High *Acropora* growth rates (Diaz-Pulido et al., 2009) may support their ongoing dominance in the Keppel Islands. Low recruitment of non-*Acropora* species may also limit competition with other taxa on Keppel Island reefs, although *Acropora* recruitment is also lower than elsewhere (Davidson et al., 2019; Thompson et al., 2021). Disturbance-sensitive coral taxa, including the *Acropora*, are forecast to be replaced by more resistant taxa on Indo-Pacific reefs under future warming scenarios (Côté & Darling, 2010; van Woesik et al., 2011), resulting in future novel coral communities (McClanahan, 2020). It is therefore unclear how long current coral communities can retain the capacity to resist and recover from disturbances as these increase in frequency and intensity in a warming world (Cai et al., 2014; Côté & Darling, 2010; Harmelin-Vivien, 2021; Heron et al., 2016; Johns et al., 2014; Timmermann et al., 1999).

Rates of ocean warming vary in space (Dunstan et al., 2018; Heron et al., 2016; Randall & van Woesik, 2015) and within the southern GBR, long-term records indicate that SSTs have increased 0.8°C since 1870 (Figure 3a). Corals here are experiencing warmer summers and winters, year on year, resulting in longer periods of summer-like temperatures and shorter winter reprieves, a pattern detected for many reefs worldwide (Heron et al., 2016). Minimum temperatures are also increasing faster than maximum temperatures, so stressful winter cold snaps that may have limited recovery or resulted in cold-water bleaching in the past (Hoegh-Guldberg et al., 2005; Hoegh-Guldberg & Fine, 2004; Howells et al., 2013), may be less problematic in the future (Schlegel et al., 2021). Shorter or less frequent winter reprieves from heat stress may also reduce the recovery capacity of corals in the future. Faster recovery of coral at reefs experiencing lower heat exposure (Figure 9), combined with high survival of Keppel Island's coral during the cooler than average autumn and winter that followed severe bleaching (Figures 3d and 7), highlight the importance of cool reprieves for coral recovery in a warming world.

High spatial resolution sea surface temperature models, such as that used here to calculate site-specific climatologies, are only available for a relatively recent window. For example, the GBR1 Hydro V2 eReefs model is only available from 2014 onwards. Heat-exposure metrics based on such recent baselines are therefore conservative and it is likely that mDHW estimates would have predicted higher heat accumulation than was calculated here, had a longer-term baseline been available (Figures 3b and 9). Despite the use of a recent baseline, this study still conservatively estimated the accumulation of 4–8 mDHWs across all sites and depths, suggesting that heat exposure was indeed severe during the 2020 marine heat wave. Reefs exposed to more than four DHWs are expected to experience significant bleaching, while widespread severe bleaching and significant coral mortality is expected on reefs exposed to eight or more DHWs (Skirving, 2020). Significant coral mortality was not recorded in this region, including on reefs experiencing almost eight mDHWs (7.95 mDHWs), indicative of high resilience in this southern GBR and in contrast to the expectation of high mortality, given the naivety of the region to recent high heat exposure (Skirving, 2020).

Models, such as GBR1, that rely on downscaling to describe fine-scale spatial patterns from those measured at broader scales can miss the heterogeneity inherent in complex and dynamic systems including coral reefs. While an extensive calibration and validation of GBR1 has been undertaken (Herzfeld et al., 2016), it is possible that some fine-scale patterns in temperature and flow dynamics within reefs may have been missed by this model. Even so, the modeled temperature data appeared to predict coral bleaching at a fine spatial scale reasonably well in a recent study (Steven et al., 2019) and were significant predictors of reef recovery in this study, suggesting that the modeled data are picking up some important aspects of variability at this scale. Further validation of these models at within-reef scales and across environments and latitudes will improve the accuracy for use in future studies.

Globally, the onset of coral bleaching is occurring at higher temperatures than previously, suggesting that directional selection for more thermally tolerant coral genotypes is underway (Sully et al., 2019). The high survival following severe heat exposure and bleaching in 2020 suggests that directional selection may already be occurring here. Indeed, repeated reductions in coral cover followed by rebounds throughout the last 30 years of disturbance events (Figure 1) support the assertion that present-day Keppel coral populations are locally adapted. Evidence of the directional selection toward more heat-tolerant Symbiodiniaceae communities in *A. millepora* populations in this region (Bay et al., 2016; Jones et al., 2008) also supports this hypothesis. Long-term temperature increases recorded in this region (Figure 3a,b) also indicate that directional section has likely been occurring in the Keppel Islands for considerably longer than the 30 years over which coral cover has been monitored in this region. Yet, recovery was fastest at sites experiencing the lowest heat stress, and survival was likely enhanced by cooler than average autumn and winter temperatures. As climate warming continues, the capacity of corals for recovery is continually being tested (Ortiz et al., 2018; Osborne et al., 2017). Frequent and severe bleaching events, such as the 2020 event reported here, highlight the importance of actions that slow and limit future warming.

AUTHOR CONTRIBUTIONS

Cathie A. Page, Line K. Bay, and Carly J. Randall conceived the study. Cathie A. Page, Christine Giuliano, and Carly J. Randall collected the data. Cathie A. Page and Carly J. Randall analyzed the data. Cathie A. Page, Line K. Bay, and Carly J. Randall planned and wrote the paper. Christine Giuliano reviewed and edited the paper. All authors read and approved the final version.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

Data (AIMS, 2022) are available from: https://doi.org/10.25845/SN2B-WS89.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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