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Size-dependent mortality of corals during marine heatwave erodes recovery capacity of a coral reef

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Abstract

For many long-lived taxa, such as trees and corals, older, and larger individuals often have the lowest mortality and highest fecundity. However, climate change-driven disturbances such as droughts and heatwaves may fundamentally alter typical size-dependent patterns of mortality and reproduction in these important foundation taxa. Working in Moorea, French Polynesia, we investigated how a marine heatwave in 2019, one of the most intense marine heatwaves at our sites over the past 30 years, drove patterns of coral bleaching and mortality. The marine heatwave drove island-wide mass coral bleaching that killed up to 76% and 65% of the largest individuals of the two dominant coral genera, *Pocillopora* and *Acropora*, respectively. Colonies of *Pocillopora* and *Acropora* ≥30 cm diameter were ~3.5× and ~1.3×, respectively, more likely to die than colonies <30-cm diameter. Typically, annual mortality in these corals is concentrated on the smallest size classes. Yet, this heatwave dramatically reshaped this pattern, with heat stress disproportionately killing larger coral colonies and equalizing annual mortality rates across the size spectrum. This shift in the size-mortality relationship reduced the overall fecundity of these genera by >60% because big corals are disproportionately important for reproduction on reefs. Additionally, the survivorship of microscopic coral recruits, critical for the recovery of corals following disturbances, declined to 2%, over an order of magnitude lower compared to a year without elevated thermal stress, where 33% of coral recruits survived. While other research has shown that larger corals can bleach more frequently than smaller corals, we show the severe impact this phenomenon can have at the reef-wide scale. As marine heatwaves become more frequent and intense, disproportionate mortality of the largest, most fecund corals and near-complete loss of entire cohorts of newly-settled coral recruits will likely reduce the recovery capacity of these iconic ecosystems.

KEYWORDS
climate change, coral recruitment, global warming, mass mortality, resilience, thermal stress

1 | INTRODUCTION

Climate change is increasing the intensity and frequency of disturbances across many ecosystems, causing mass mortalities of foundation species (Anderegg et al., 2013; Hughes et al., 2017) that provide essential ecosystem services (Ellison et al., 2005). Many foundation organisms, such as corals and trees, are particularly vulnerable to changing disturbance regimes because they are slow-growing and long-lived. In forests, large trees, which typically have low annual mortality (Muller-Landau et al., 2006; Thomas, 1996), often have the highest rates of mortality during disturbances like intense drought (Bennett et al., 2015; Van Nieuwstadt & Sheil, 2005). These larger trees are more likely than smaller trees to experience failure of vital physiological processes due to deterioration of their internal water-conducting tissues, resulting in their death (Anderegg et al., 2012; Rowland et al., 2015) and the loss of their unique and irreplaceable ecological roles (Lindenmayer et al., 2012). Like trees in forests, corals are the long-lived foundation organisms of tropical reefs, and their annual mortality rates decrease with increasing size (Hughes & Connell, 1987). However, much like the drought in forests, marine heatwaves are likely altering the typical patterns of coral mortality on tropical reefs, suggesting commonalities in how climate change is impacting foundation species.

Under climate change, marine heatwaves are driving more frequent, intense coral bleaching events (Hughes et al., 2017; Loya et al., 2001) where the mutualism between corals and their endosymbiotic algae, Symbiodiniaceae, breaks down, often resulting in coral death (LaJeunesse et al., 2018; Lesser, 2011). Small-scale field studies and experiments suggest that, within a given taxon, larger colonies may be more sensitive to thermal stress than small colonies. For example, larger colonies can exhibit higher bleaching prevalence (proportion of colonies that are bleached; Pratchett et al., 2013), higher bleaching severity (proportion of an individual colony that bleached; Brandt, 2009), and more severe bleaching-induced mortality (Shenkar et al., 2005) than smaller conspecifics. Further, juvenile corals (typically defined as the smallest colonies visible on the benthos up to 5 cm) appear to be resistant to bleaching, even during severe heatwaves that result in high mortality of adult conspecifics (Bena & Van Woesik, 2004; Depczynski et al., 2013; Loya et al., 2001). Although there is increasing evidence that larger corals may be more susceptible to bleaching and mortality, we know little about how this size-dependent mortality will impact coral communities and the likelihood that they recover after marine heatwaves.

Although juvenile corals (~1–5-cm diameter) may have higher resistance to bleaching than adult corals, they are not the smallest corals on the reef. Coral recruits (coral spat; ~500 μm–1 cm) are the newly established members of a coral community and are typically undetectable to the naked eye for the first weeks to months of their lives. Limited data from laboratory experiments suggest that coral recruits may be highly sensitive to thermal stress (Fourney & Figueiredo, 2017; Nozawa & Harrison, 2007). However, because of their microscopic size, coral recruits are difficult to observe in situ, and, to the best of our knowledge, no published data exist on the survivorship of coral recruits in situ during a marine heatwave. Therefore, we have a very limited understanding of how coral recruits fare during bleaching events. Coral recruits are extremely sensitive to external stressors and have high rates of post-recruitment mortality early in life (Penin et al., 2010). Understanding how these events may drive size- and stage-specific mortality of foundational coral taxa is central to our understanding of how reef ecosystems will fare in a changing climate.

In the Austral summer of 2019, Moorea, French Polynesia, experienced a prolonged marine heatwave with *in situ* ocean temperatures consistently above the long-term mean from December 2018 until July 2019. In response to this heatwave, we examined how bleaching-induced mortality of the two dominant genera of corals varied with coral size. The aim of our study was to describe the impacts of bleaching and mortality around the island of Moorea and to evaluate the hypothesis that larger corals of the two dominant genera experienced higher rates of mortality than smaller corals. We then evaluated the potential for size-dependent bleaching and mortality to have cascading impacts on coral fecundity and recruitment, two factors closely tied to the resilience of reef communities.

We first conducted island-wide surveys on >2200 individual corals and binned them into three coarse size classes to examine overall patterns of coral mortality and size at the island scale. Then, we chose one representative site on the north shore to examine finer-scale relationships between coral size and mortality where we collected data on >2700 corals measured to the nearest centimeter. Next, we used long-term demographic data to ask whether coral mortality from this bleaching event resulted in different patterns of size-dependent mortality than are typical in years without bleaching events. We then estimated how size-dependent patterns of coral mortality following the heatwave influenced coral fecundity. We used published relationships between colony size, surface area, and gamete production to estimate how the loss of corals following this event changed the quantity of gametes produced by the dominant coral taxa. Finally, we examined how this marine heatwave influenced the survival of the most recently settled corals by repeatedly surveying coral recruits *in situ* before and after the heatwave. Our goal was to not only examine the effects of marine heatwaves on corals across the size spectrum but to understand how severe bleaching events may impact the future dynamics of coral communities, specifically by disproportionately affecting the life stages most important for reproduction and recruitment of new individuals.

2 | MATERIALS AND METHODS

2.1 | Ocean temperature data

Ocean temperature data (Figure 1a) were collected continuously from 2005 to 2019 at six sites on the outer reef of Moorea as part of the Moorea Coral Reef LTER time series (LTER 1-6, see Figure S1 for site locations; Leichter et al., 2019). At each site, a bottom-mounted thermistor (Seabird SBE 39) recorded temperature at 20 min intervals at 10 m water depth, which we then used to calculate the average temperature at each site for each day of the 14-year time series. We used data through 31 July 2018 to analyze long-term mean temperature trends in Moorea. We first calculated the mean ocean temperature at each site on each day of the time series. We then used these daily means for each site to calculate the mean ocean temperature across all sites ±1 standard deviation for each day in a 365-day year. To analyze temperature trends for August 2018–2019,

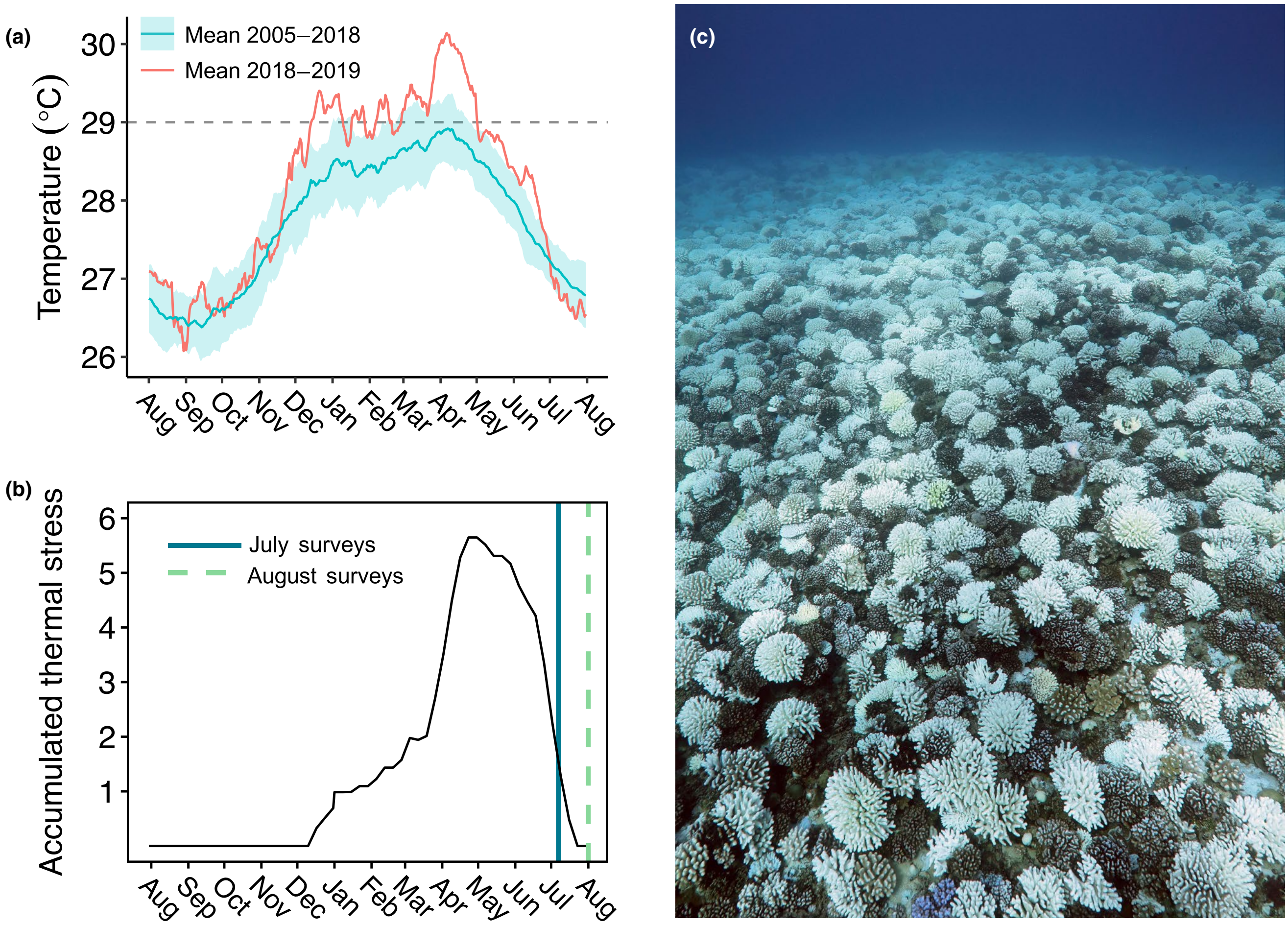

Photo: Andrew Thurber

FIGURE 1 Long-term ocean temperature trends and thermal stress events in Moorea. (a) Long-term ocean temperature trends versus temperatures in 2018–2019 on the outer reef of Moorea, measured in situ using thermistors mounted on the reef at 10-m depth at six sites around the island. Data from a subset of four of the six sites (at least one from each of the three sides of the island) had continuous data throughout 2018–2019, and, therefore, we considered only those four sites in our analysis of temperature trends for this year. Mean ocean temperature from 2005 to 2018 is shown in blue and shading is ±1 standard deviation. (b) Accumulated thermal stress in 2018–2019. (c) The severely bleached coral community at 10-m depth on the outer reef in early May 2019. Photo credit Andrew Thurber [Colour figure can be viewed at wileyonlinelibrary.com]

we considered data from 1 August 2018–31 July 2019. A subset of four of the six LTER sites (at least one from each of the three sides of the island) had continuous data throughout this time series, and, therefore, we considered only those four sites in our analysis of temperature trends for this year. Using the same approach as the long-term trends, we first calculated the mean temperature for each day at each site, and then averaged the daily data at the four sites to calculate the mean daily temperature for this year (Figure 1a).

Thermal stress that corals experience is a function of the magnitude and duration of warm water events. We used the site × day mean temperature from August 2018 to August 2019 to calculate accumulated heat stress throughout this bleaching event. In Moorea, 29.0°C is the maximum monthly mean (MMM) temperature, a known threshold at which corals accumulate thermal stress in Moorea (Pratchett et al., 2013). We quantified accumulated heat stress as a 12-week running sum of mean weekly temperatures for which the mean water temperature exceeded 29.0°C. This is calculated similarly to NOAA Degree Heating Weeks (or °C-weeks; Liu et al., 2003; Pratchett et al., 2013) which accumulate when the weekly mean water temperature is ≥MMM +1°C, except our metric accumulated heat stress any week when the water temperatures were +0.1°C >MMM (29.0°C). We calculated accumulated heat stress for 2018–2019 (Figure 1b) and throughout our 14-year time series (Figure S2). In 2018–2019, accumulated heat stress at 10 m on the outer reef peaked at 5.6°C weeks which far exceeded the magnitude of other thermal stress events on the outer reef in Moorea in the last 14 years (Figure S2). All statistical analyses and data visualization were performed in R (Version 3.5.2) and figures were made using the ggplot2 package (Wickham, 2010).

2.2 | Island-wide patterns in coral bleaching and mortality

All benthic surveys were conducted along the 10-m isobath on the outer reef of Moorea. On 9–15 July 2019, approximately 2 months after the peak of accumulated heat stress, two divers on SCUBA conducted coral bleaching and mortality surveys (Figure 2) at six sites on the outer reef, with two sites on each side of the island (Figure S1; Speare et al., 2021). *Pocillopora* were substantially more abundant than *Acropora* so we employed slightly different survey methods for the two genera. At each site, divers surveyed *Pocillopora* and *Acropora* along two 50-m transects, in which divers quantified bleaching and mortality for every *Pocillopora* that intercepted the transect. *Pocillopora* corals exhibit high phenotypic plasticity and cannot be reliably identified in the field based on morphology (Marti-Puig et al., 2014; Pinzón et al., 2013); therefore, we identified pocilloporid corals to genus.

Acropora was much less abundant than *Pocillopora* so divers collected data for every *Acropora* within 1-m wide swath along the transect. There are at least 12 species of *Acropora* in Moorea (Carroll et al., 2006), at least eight of which are common on the outer reef (*Acropora retusa*, *Acropora cerealis*, *Acropora hyacinthus*, *Acropora globiceps*, *Acropora lutkeni*, *Acropora nasuta*, *Acropora elseyi*, and *Acropora horrida*). *A. elseyi* and *A. horrida* are two species that have delicate branching morphologies and reproduce frequently by asexual fragmentation and reattachment. These species were uncommon in our dataset, but we omitted all individuals of these two species from our analyses for two reasons. First, both species fragment easily and therefore change the size, and second, clusters of reattached fragments likely originated from one individual and, therefore, do not represent independent samples. Several of the common species (*A. retusa*, *A. cerealis*, *A. lutkeni*, *A. globiceps*, *A. nasuta*) share similar morphological characteristics and are difficult to identify in situ, particularly when colonies are bleached or dead and overgrown by algae. We pooled all *Acropora* in our dataset and considered patterns of *Acropora* mortality at the genus level because of the challenges of identifying dead individuals to species. While we recognize that pooling these taxa by genus may obscure possible differences in bleaching and mortality among species, pooling data by genus is common for ecological studies of corals at the landscape- and regional-scale, including studies that investigate size-specific impacts of disturbances on corals (Dietzel et al., 2020; Gilmour et al., 2013).

Divers quantified bleaching and mortality for each individual coral colony ≥5 cm in diameter, which totaled 2209 corals (1446 *Pocillopora* and 763 *Acropora*). Each colony was binned into one of three size bins (5–9, 10–29, 30+ cm), and the percent that was

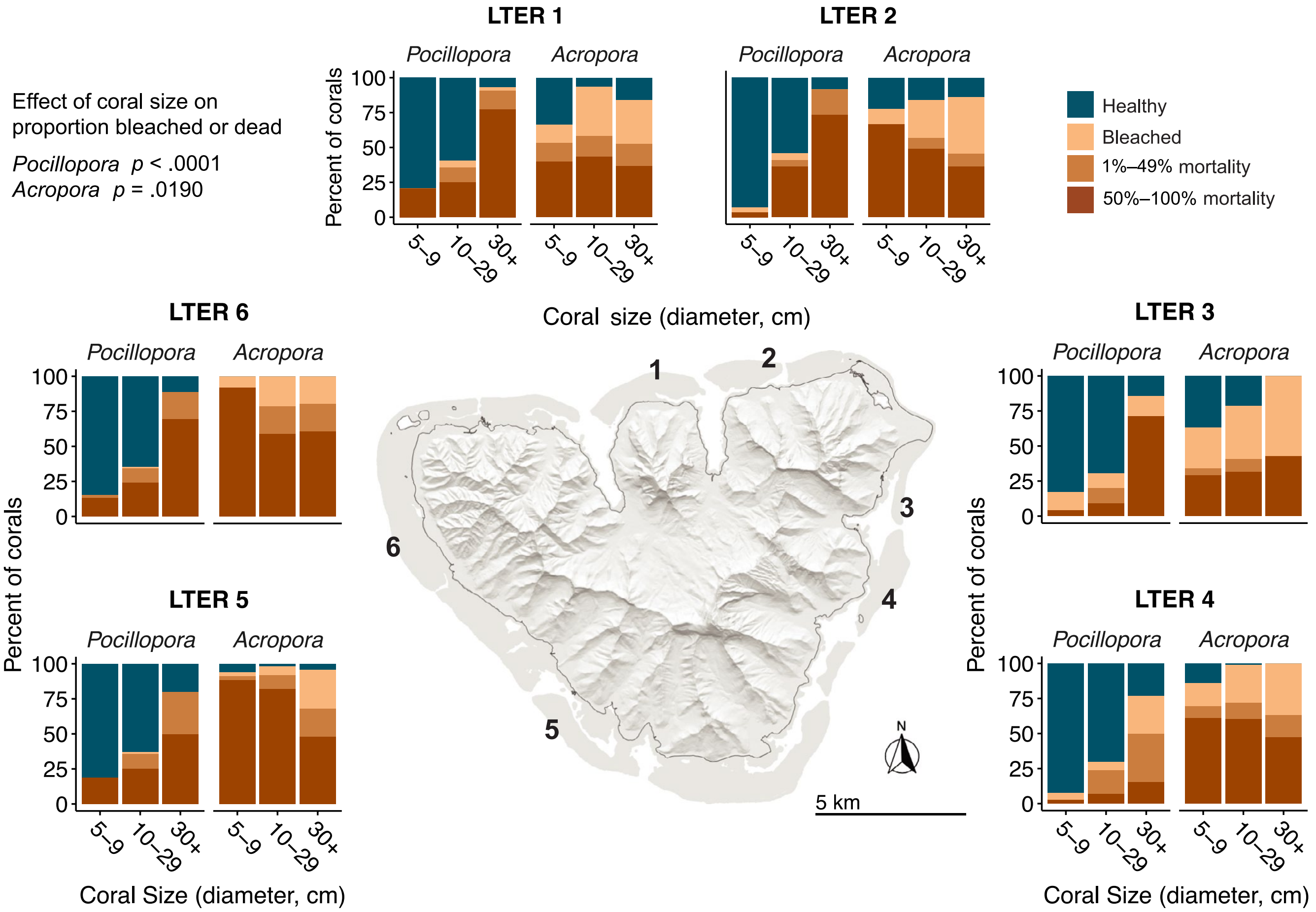

FIGURE 2 Island-wide patterns of coral bleaching and mortality. The proportion of individuals of the two dominant genera (*Pocillopora* and *Acropora*) that appeared to be healthy, were bleached, or had 1%–49% mortality or 50%–100% mortality. Data on bleaching and mortality were collected for >2200 individual colonies by divers in situ at six sites on the outer reef of Moorea. Numbers on the map indicate the location of each of the six sites on the outer reef [Colour figure can be viewed at wileyonlinelibrary.com]

bleached and recently dead was then estimated for each colony. Portions of colonies were considered "recently dead" if they were visibly colonized by turf algae but not yet colonized by macroalgae (see Figure S3). We categorized each coral in our surveys into one of four categories: Bleached (if any portion of the coral was bleached but there was no mortality), 1%–49% mortality, 50%–100% mortality, or healthy (if no bleaching or mortality was present) and then calculated the mean proportion of corals in each category for each site and size class. Because the means of each category are not independent, we only tested for the effects of coral size on the proportion of colonies that were impacted by the heatwave (combining Bleached and Dead categories) for each genus. For each genus, we used linear mixed-effects models to ask whether colony size (as an ordinal variable where 5–9, <10–29, <30+ cm) had a significant effect on the proportion of corals that were impacted (i.e., Bleached or Dead) using the *lmer()* function in the *lme4* package (Bates et al., 2015). Differences in thermal stress at different sites could cause variation in the prevalence of bleaching and mortality; therefore, we included site as a random effect in each of our models.

2.3 | Fine-scale patterns in size-dependent coral mortality

To better understand how bleaching and mortality varied with coral colony size, we conducted more size-explicit coral bleaching and mortality surveys of 2704 corals (2395 *Pocillopora* and 309 Acropora) using finer scale resolution of colony size (Figure 3) from 30 July–7 August 2019 (Speare et al., 2021). Due to the time-intensive nature of these surveys, we conducted them only at 10-m depth at one site (the LTER Experimental Site, see Figure S1) on the outer reef of the north shore of Moorea. Two SCUBA divers conducted ten 15 × 1 m-belt transects in which they visually estimated bleaching and mortality for every colony >5 cm diameter for 2147 corals using the same methods as described earlier. For these surveys, we measured the longest diameter of each colony to the nearest centimeter using a meter stick with centimeter markings. We then surveyed the same transects a second time and expanded the width to 2 m (15 × 2 m belt transects) to quantify bleaching and mortality of juvenile corals 1–5 cm diameter (557 corals). We measured the diameter of each coral to the nearest centimeter using a ruler, and visually estimated the percent of the colony that was bleached and recently dead. To visualize the population size structure prior to bleaching-induced mortality, we generated size-frequency distributions (binned in 5-cm increments) for all colonies that were healthy, bleached, or recently dead at the time of the surveys. We normalized counts of corals to the area surveyed to calculate size-frequency distributions for *Pocillopora* and *Acropora* (Figure S4c,d). To assess the relationship between colony size and the probability of mortality we calculated the proportion of individuals that had at least 50% partial mortality for each 5-cm size class (Figure 3a,b). For *Pocillopora* and *Acropora*, we evaluated the relationship between colony size and the probability of having at least 50% partial mortality using logistic regression (Figure 3a,b).

For corals that exhibited partial colony mortality, most of the mortality was concentrated on the ends of the branches, and generally, the only remaining live tissue was deep within the branches and around the base where there is limited access to light (see Figure S3). Additionally, much of the remaining live tissue on colonies with partial mortality was still bleached at the time of our surveys (see Figure S3). Coral colonies often exhibit delayed bleaching-induced mortality months after thermal stress subsides (Brown & Phongsuwan, 2012; Oxenford et al., 2008); therefore, it is likely that colonies with severe partial mortality continued to lose live tissue after our surveys. Thus, we assumed that colonies with ≥50% partial mortality in our August surveys would be unlikely to survive long-term. We conducted follow-up surveys on 15–16 October 2019 to confirm this assumption. Here, we used the same methods as described above to survey >500 individual colonies of *Pocillopora* and >200 individuals of *Acropora* on the north shore (see Table S1 for the number of corals surveyed in each sampling period). We calculated the proportion of corals with 100% mortality for each 5-cm size class and evaluated the relationship between colony size and the probability of 100% mortality using logistic regression (Figure 3c,d).

2.4 | Annual patterns of size-dependent mortality

Demographic surveys of coral were conducted at 10-m depth at four of the six LTER sites (LTER 1, 2, 4, and 5, see Figure S1) from 2013 to 2019. At each site, four permanent 5-m^2 quadrats were established and all *Acropora* corals were mapped and measured (Lenihan et al., 2019). Nested within each 5 m^2 quadrat was a 1 m^2 quadrat where all *Pocillopora* corals were mapped and measured. Each coral was mapped on an *x*, *y*, *z* coordinate system, which served as a unique identifier for each coral and enabled tracking of individuals annually (Kayal et al., 2018). We measured the longest diameter of each colony to the nearest centimeter each year. These surveys resulted in 3001 observations of annual survivorship from 2013 to 2019, of which 2179 were for *Pocillopora*, and 822 were for *Acropora*. These annual surveys were used to calculate the probability of annual mortality of *Pocillopora* and *Acropora* across the size spectrum. In our data analysis, we used the size of the coral in the previous year (its last known size) to predict the probability of mortality in that year. Corals that died were removed from the dataset for all subsequent years. Corals were not surveyed in 2017; so, data from 2016 to 2018 represent mortality over a 2-year period.

We analyzed the relationship between colony size and the probability of mortality between years using generalized linear mixed models (Figure 4a,b). We were interested in evaluating how this relationship between coral size and mortality may differ between high thermal stress years and low thermal stress years. To do this, we assigned each year a categorical variable of "year type" with categories of either "low thermal stress" (2013–2014, 2014–2015, 2015–2016, 2016–2018) or "high thermal stress" (2018–2019). We then used

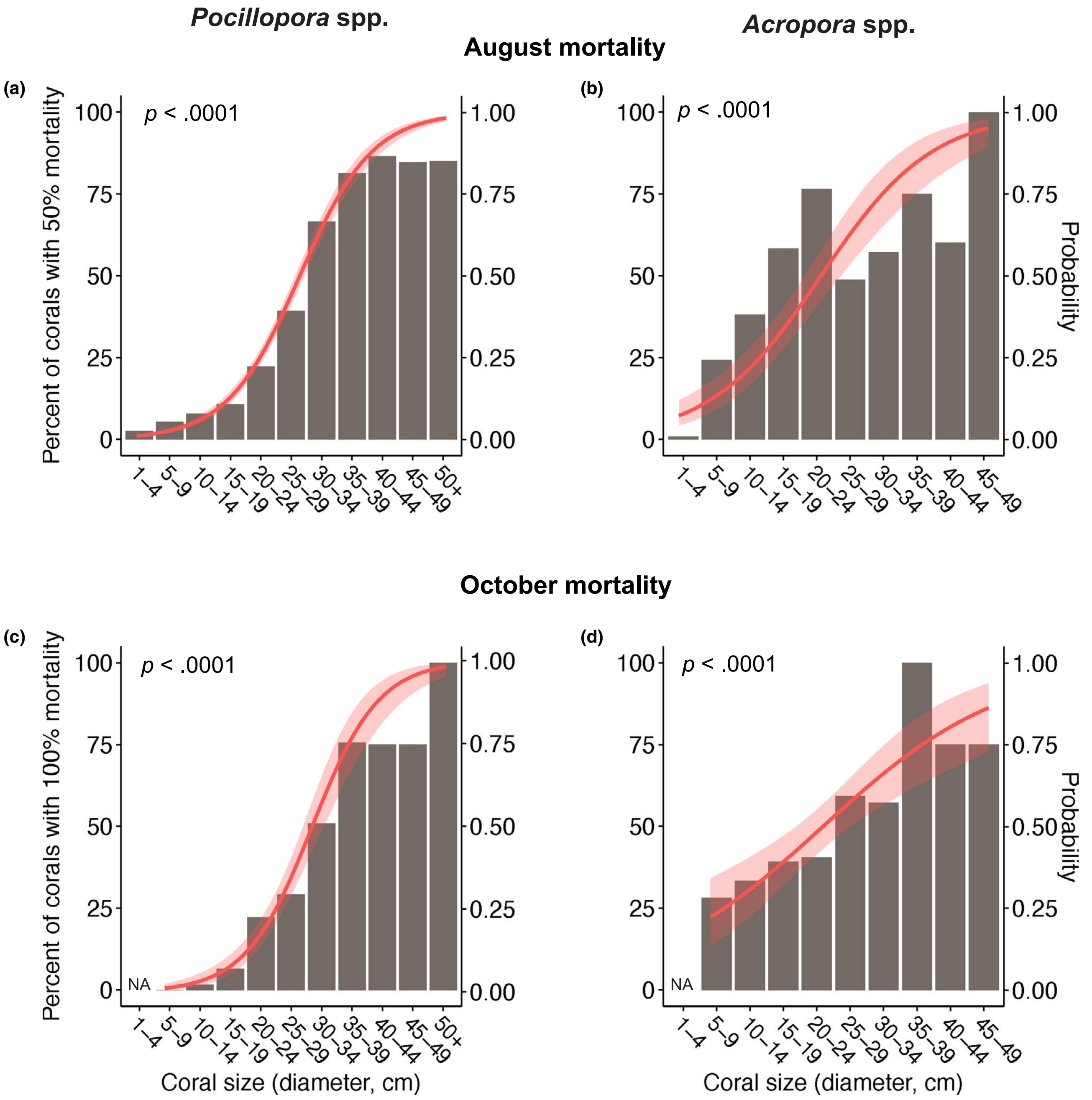

FIGURE 3 Relationships between coral colony size and probability of mortality during the 2018–2019 bleaching event. The percent of individuals of *Pocillopora* and *Acropora* in each size class with at least (a, b) 50% mortality and (c, d) 100% mortality following the bleaching event. The red line is the probability of having at least 50% mortality (a, b) or 100% mortality (c, d) via logistic regression. *p* values from logistic regression [Colour figure can be viewed at wileyonlinelibrary.com]

generalized linear mixed models (GLMMs, R package "lme4") with a binomial distribution and fit models by maximum likelihood using the Laplace approximations (Bolker et al., 2009; Raudenbush et al., 2000). We modeled the probability of coral mortality using fixed effects of coral size, year type, and their interaction, and included random effects of site and year. We then used χ^2 likelihood ratio tests to evaluate the significance of fixed effects (Bolker et al., 2009). As a more conservative approach, we also evaluated the significance of fixed effects using the parametric bootstrapping method (R package "pbkrtest"; Halekoh & Højsgaard, 2014), but the significance patterns were quantitatively the same as results from the χ^2 tests in all cases, so we only report the χ^2 results here. Separate analyses were computed for *Pocillopora* and *Acropora*.

Throughout our demographic data collection, the outer reefs of Moorea were recovering from catastrophic disturbances from 2007 to 2010 (corallivorous crown-of-thorns seastar outbreak and a cyclone) that reduced coral cover to <1%. Therefore, all of the corals in our initial surveys in 2013 were newly recruited juveniles, and population size structure shifted strongly from juvenile to adult size classes throughout the duration of our surveys (Figure S5). We restricted analysis of

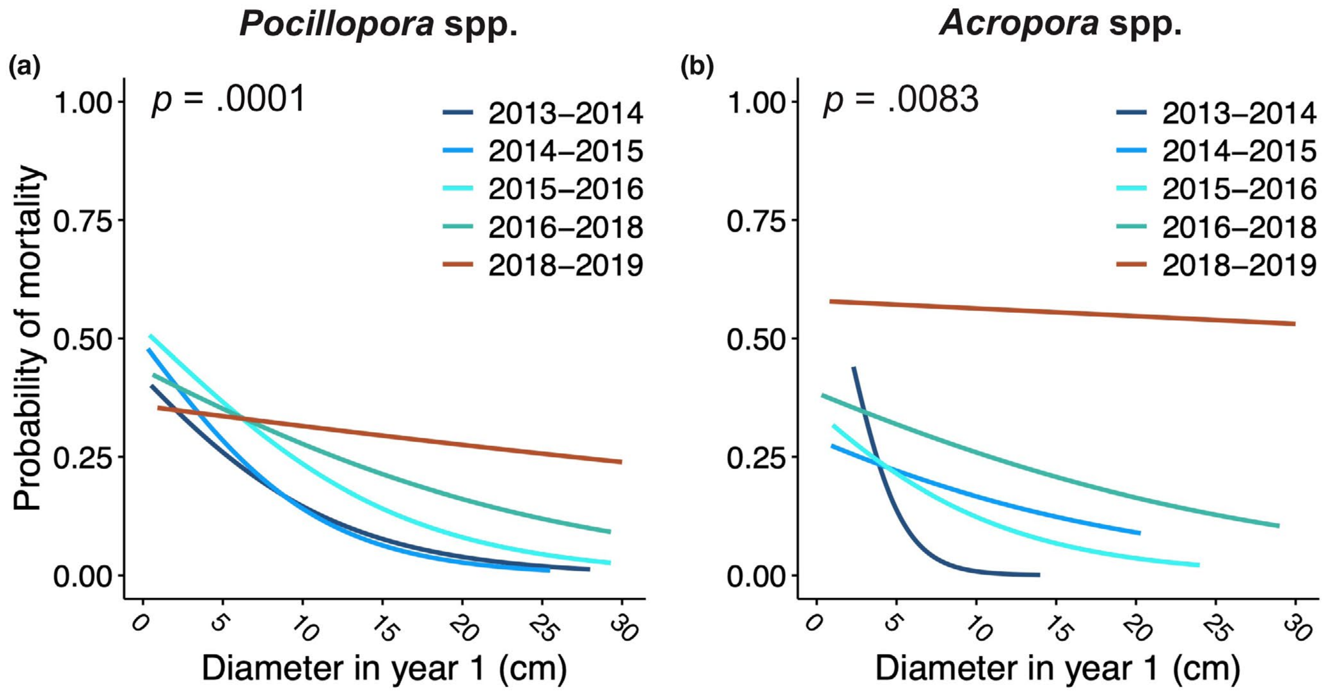

FIGURE 4 Relationship between coral colony size and annual mortality patterns in low thermal stress years (2013–2018) and a high thermal stress year (2018–2019). Annual mortality curves for (a) *Pocillopora* and (b) *Acropora* from 2013 to 2019. The *x*-axis is colony size in year 1 and the *y*-axis is the probability of mortality from year 1 to year 2. *p* values are for the Size × Year Type interaction in the generalized linear mixed model comparing low versus high thermal stress years. Note that coral mortality was not sampled in 2017 so the 2016–2018 line represents mortality over 2 years [Colour figure can be viewed at wileyonlinelibrary.com]

our demographic data to individuals ≤30-cm diameter because there were no corals >30 cm in our initial surveys, and small numbers in our surveys up until 2018. Therefore, there were not enough individuals >30 cm in the first several years of our surveys to evaluate differences in survival of the largest individuals between high thermal stress (2018–2019) and low thermal stress years (2013–2018).

2.5 | Estimating coral fecundity

We used our size-explicit coral bleaching and mortality survey data (August 2019) from the LTER Experimental Site to estimate coral fecundity before and after this mortality event for *Pocillopora* and *Acropora*. There are thought to be six common species of *Pocillopora* in Moorea (Edmunds et al., 2016), but corals in the genus *Pocillopora* exhibit significant phenotypic plasticity and cannot be identified reliably to species in the field based on morphology (Marti-Puig et al., 2014; Pinzón et al., 2013). For purposes of our fecundity estimates, we considered the fecundity of *Pocillopora* at the genus level, recognizing that there are likely differences among the cryptic species in this genus. In contrast, there are at least 12 species of *Acropora* in Moorea (Carroll et al., 2006). We acknowledge that these are distinct species, however, relationships between colony size and live tissue surface area have not been established at the species level. Reliable estimates of the live surface area of corals can be made based on coral morphology (i.e., branching, massive, encrusting; House et al., 2018), and estimates of gamete output are only available for certain species. Therefore, we estimated *Acropora* fecundity at the genus level using established relationships between colony size and surface area (House et al., 2018) and estimates of gamete output per unit coral surface area averaged at the genus level (Table S2).

For each genus, we estimated fecundity before and after the bleaching event. Using the coral bleaching and mortality surveys from August 2019, we made two estimates of coral fecundity for each genus. In the Pre-Bleaching estimate, we assumed that all individuals that were healthy, bleached, or recently dead (≥50% colony mortality) at the time of our surveys were alive and reproductive prior to the bleaching event. For the Post-Bleaching estimate, we assumed that all individuals that had ≥50% colony mortality at the time of our surveys ultimately died and were no longer reproductive. This assumption is reasonable given that the majority of the colonies that had 50% mortality in August had 100% mortality by October (Figure 3). For each estimate, we only included individuals that were likely to be reproductive based on previously published size thresholds. For *Pocillopora*, we assumed that the size of the onset of sexual maturity is 14-cm in diameter, given existing data for *Pocillopora meandrina* (Stimson, 1978). For *Acropora*, most colonies at least 14 cm in diameter are reproductive (Hall & Hughes, 1996). Therefore, for both genera, we included only colonies ≥14-cm diameter for each fecundity estimate.

For each individual in our surveys, we used a calibration curve to estimate coral planar surface area from the coral diameter (Table S2, described below) and then used published relationships between colony diameter and live surface (House et al., 2018) area to estimate fecundity of each colony in our dataset. Corals are colonial animals and individual polyps reproduce by releasing sexually produced gametes (Richmond & Hunter, 1990). Therefore, the reproductive potential of a given colony can be estimated as a function of the number of individual polyps of the colony (sensu Tsounis & Edmunds, 2016). The number of polyps per colony scales linearly with the surface area of tissue of the colony, therefore, we can estimate the fecundity of each colony by calculating colony surface area and multiplying it by the number of eggs released per unit surface area.

We first created calibration curves to convert colony diameter to planar (2D) surface area using top-down photos of individual colonies (Table S2). For each colony, we measured colony diameter and traced the perimeter to calculate planar area in ImageJ. We then created calibration curves of diameter to planar surface area for colonies of *Pocillopora* and *Acropora* separately. We then estimated the live tissue area of each colony from the planar surface area of each colony using published relationships (House et al., 2018). Next, we used our estimates of live tissue area for each colony to estimate fecundity of each colony (expressed as eggs cm^{-2} year^{-1} for *Pocillopora*, and oocytes cm^{-2} year^{-1} for *Acropora*) based on published estimates of fecundity per unit coral surface area (Kotb et al., 2018; Tsounis & Edmunds, 2016). See Table S3 for parameter estimates.

Using these relationships between colony diameter, surface area, and gamete output, we estimated the fecundity of each coral in our dataset and propagated error using a Monte Carlo simulation framework. For each run of the simulation, we used a random draw of each parameter estimate (assuming a normal distribution of standard errors, which were estimated in original studies given in Table S2) and applied those parameters to all individuals in the genus to estimate individual colony fecundity. The fecundity of individual colonies was summed and divided by the total area surveyed in the fine resolution surveys to estimate annual area normalized genus-level fecundity (eggs or oocytes m^{-2} year^{-1}) for each run of the simulation. We then calculated the relative change in fecundity as the difference between pre-bleaching and post-bleaching fecundity divided by the pre-bleaching fecundity. We repeated this process 1000 times. The mean was then calculated as the average fecundity of 1000 runs of the simulation with 95% confidence intervals (Figure 5a,c). We also summed fecundity for each coral size class for each run of the simulation. We then calculated the relative contribution that each size class made to total fecundity at the genus level before and after the bleaching event (Figure 5b,d).

2.6 | Survivorship of coral recruits

We assessed the survivorship of coral recruits in situ during the bleaching event using 64 coral limestone settlement tiles deployed at 10 m on the outer reef at the LTER Experimental Site (see Figure S1; Speare et al., 2021). Coral settlement tiles were deployed in August 2018 and accumulated naturally-settled recruits throughout the timeframe of our study. Coral recruits are notoriously difficult to identify while alive so it was not possible to identify the recruits on our tiles to genus. However, prior data show that typically most recruits on the north shore of Moorea are Pocilloporidae and some Acroporidae (Edmunds, 2018). The overwhelming majority of *Pocillopora* coral species and all *Acropora* species on the outer reef of Moorea are broadcast spawning species; therefore, it is unlikely that different modes of reproduction influenced the patterns of recruitment on our tiles.

During 23–31 March 2019, coral settlement tiles were collected from the reef daily in groups of eight and transported to the wet lab at the Richard B. Gump research station in a cooler of seawater. The surfaces of each tile were digitally photographed (Olympus Stylus Tough TG-4 camera). We searched each tile for coral recruits using a dissecting microscope, and the location of each individual recruit was marked and numbered on the digital photos of each tile. Tiles were kept submerged in seawater throughout this process and returned to the reef within 24 h of collection. This method has been used to successfully track the fate of individual coral recruits in the field without significant handling effects (Price, 2010).

Tiles were returned to the reef for 4 months and collected again from 14 to 30 July 2019, after the thermal stress event was over. Of the 64 tiles originally deployed, 34 tiles had 1–9 coral recruits per tile in March 2019. We searched these tiles again for coral recruits, looking specifically in locations where recruits were previously mapped. Recruits that were mapped in March were then scored as either Alive or Dead in July. For the tiles that had coral recruits, we computed mean survival for each tile ($n = 34$). In 2017, we tracked coral recruit survival during the same timeframe (March–July) using the same methods ($n = 12$ tiles). We, therefore, can compare the recruit survival data in 2019, a year with high prolonged thermal stress, to recruit survival in 2017, a year with low thermal stress (Figure 6). We first compared survivorship at the tile level in 2017 versus 2019 using a *t* test. Next, we asked whether there was a relationship between tiles having at least one surviving recruit and the year (2017 or 2019) using a contingency test as a more conservative approach.

The settlement tiles that were scored in 2019 were part of factorial in situ experiments that artificially manipulated herbivore abundance (via herbivore exclusion) and nutrient enrichment (via nutrient diffusers filled with Osmocote slow-release fertilizer), and adult coral community disturbance (adult corals removed or adult coral community intact). We used a linear mixed-effects model to test the null hypothesis that the experimental treatments (herbivore exclusion, nutrient enrichment, and coral disturbance) had no effect on coral recruit survival. This was a blocked factorial experiment, therefore, we included the experimental block as a random effect. There was no effect of herbivore exclusion, nutrient enrichment, or coral disturbance on coral recruit survival during this thermal stress event (Table S3). We, therefore, conclude that the effects of thermal stress overwhelmed any effects of the experimental treatments.

3 | RESULTS

3.1 | Magnitude of thermal stress

Moorea experienced a prolonged marine heatwave in the Austral summer of 2019. From December 2018 until July 2019, the ocean temperature at 10-m water depth (measured in situ) was consistently

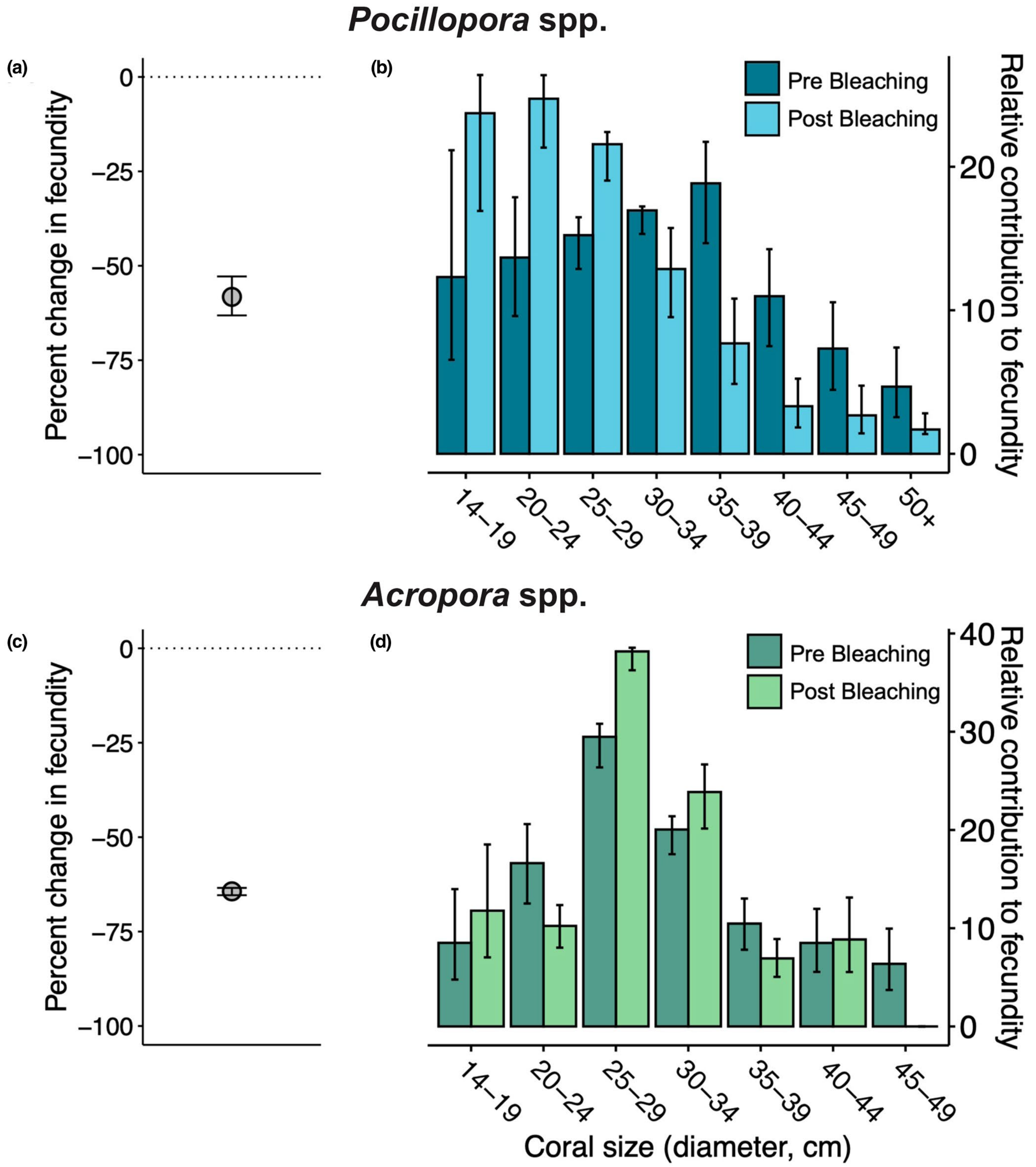

FIGURE 5 Fecundity estimates for *Pocillopora* and *Acropora* before and after the bleaching event. Estimated change in genus-level fecundity ±95% confidence intervals for *Pocillopora* and *Acropora*, respectively (a and c). The relative contribution to total fecundity ±95% confidence intervals (Pre and Post Bleaching) for each size class of individuals for *Pocillopora* and *Acropora*, respectively (b and d). Data from the August 2019 bleaching and mortality surveys were used to estimate population fecundity (a–d). All fecundity estimates were standardized to the area surveyed, therefore, differences between pre and post bleaching fecundity reflect changes in fecundity based on the loss of corals in each size class [Colour figure can be viewed at wileyonlinelibrary.com]

above the long-term mean ocean temperature by at least one standard deviation (Figure 1a). From 14 December 2018 until 1 May 2019, ocean temperatures were above 29.0°C, which is the threshold often used for predicting the accumulation of thermal stress in corals in Moorea (Pratchett et al., 2013), for 115 of 139 days, including 63 consecutive days from 28 February until 1 May 2019. These sea

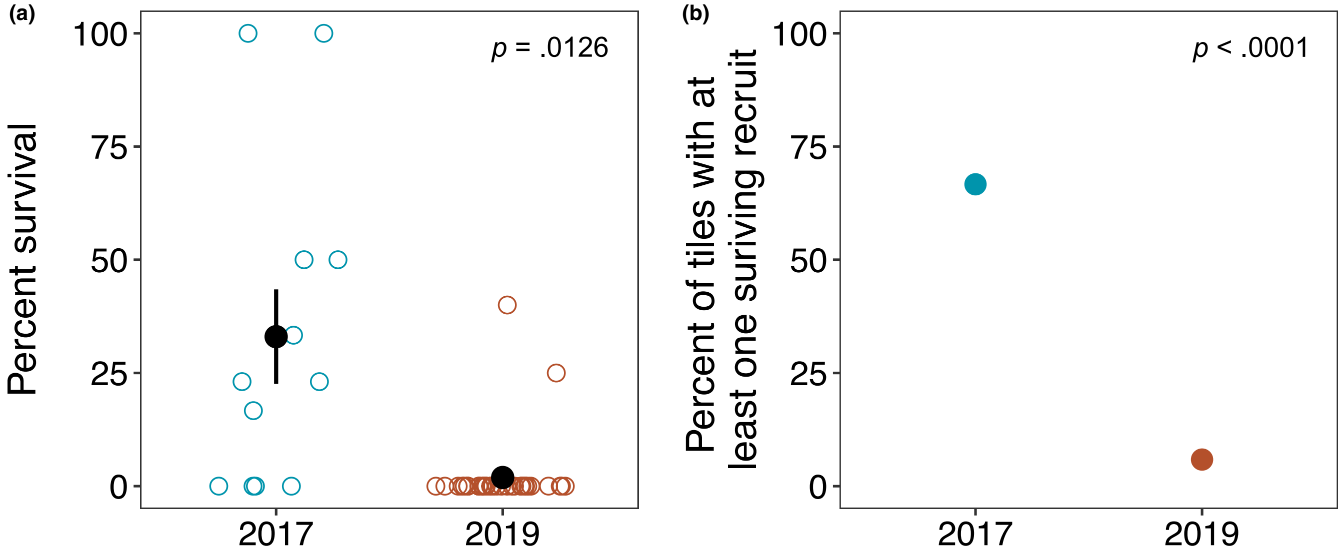

FIGURE 6 Survivorship of coral recruits under high thermal stress during the marine heatwave compared to a year with low thermal stress. (a) Survival of coral recruits (individuals 1–3 mm in diameter and <1-year-old) in 2017 (a year with low thermal stress) and during the marine heatwave of 2019. Colored data points are mean survival per settlement tile ($n = 12$ tiles in 2017 and $n = 34$ tiles in 2019). Black points (lines are ±SE) are the overall mean survival calculated from individual tile means for March–July of 2017 and 2019. *p* value from the two-tailed *t* test. (b) Percent of tiles with at least one surviving coral recruit in 2017 and 2019. *p* value from contingency test [Colour figure can be viewed at wileyonlinelibrary.com]

surface temperatures resulted in a maximum of 5.6-degree weeks of accumulated thermal stress (defined as accumulated degrees above 29.0°C during a 12-week period, Figure 1b; Liu et al., 2003; Pratchett et al., 2013) in late April. This level of thermal stress is one of the highest seen on these reefs over the past 30 years (Figure S2; Leichter et al., 2019; Pratchett et al., 2013).

3.2 | Island-wide patterns of coral bleaching and mortality

Prior to the thermal stress event, coral cover on the forereefs of Moorea ranged from 13 to 80% (mean 47%) at 10-m water depth across six sites around the island that are part of the Moorea Coral Reef Long Term Ecological Research (MCR LTER) time series (see Figure S1 for site locations). *Pocillopora* spp. and *Acropora* spp. were the two most abundant genera, representing 52%–81% (mean 63%) and 4%–20% (mean 10%) of the coral community, respectively (Edmunds, 2020). In early July 2019, we conducted bleaching and mortality surveys using coarse colony size bins (5–9, 10–29, 30+ cm diameter) at 10-m depth at each of these six sites. By this time, the marine heatwave had passed as ocean temperatures were 26.7°C, well below the 29.0°C threshold for accumulating thermal stress (Figure 1a,b).

In our survey of >2200 individual corals, we found that the marine heatwave drove strong size-dependent patterns in bleaching and mortality for the two dominant genera of corals (Figure 2). Although ocean temperatures had cooled considerably since their peak in late April, 47% of remaining live *Acropora* (but only 6% of *Pocillopora*) were still bleached in early July. There was also extensive recent mortality for both genera, indicating that bleaching had been widespread and intense. On average, 46% of *Pocillopora* and 89% of *Acropora* colonies (≥5-cm diameter) showed some bleaching or partial mortality in early July, and 25% of *Pocillopora* and 54% of *Acropora* colonies had at least 50% partial mortality (Figure 2). At the island-wide scale, the proportion of colonies impacted with either bleaching or mortality was significantly skewed toward the largest size classes for *Pocillopora* and *Acropora* (mixed-effects model $p < .0001$ and $p = .0190$, respectively), although the strength of this effect varied somewhat across sites (Figure 2).

3.3 | Fine-scale patterns of size-dependent coral mortality

To more thoroughly examine the impact of bleaching-induced mortality across the size spectrum of corals, we conducted additional size-explicit surveys of >2700 corals on the north shore of Moorea in August 2019, including individuals from 1-cm diameter juveniles to the largest adults (>50 cm diameter; Figure 3a,b, see Table S1 for the number of corals surveyed in each size class). At the time of these surveys, there was a high prevalence of severe partial mortality (≥50% of the colony dead). Similar to our island-wide surveys using coarse size bins, our size-explicit surveys of coral mortality in August 2019 showed that for both *Pocillopora* and *Acropora* larger corals were significantly more likely to have at least 50% partial mortality than smaller corals (Figure 3a,b, and logistic regression; $p < .0001$ for both *Pocillopora* and *Acropora*). For *Pocillopora*, 76% of individuals ≥30-cm diameter had at least 50% partial mortality, compared with 17% of individuals <30-cm diameter. *Pocillopora*

≥30-cm covered >40% of the benthos (Figure S3a,b); therefore, the loss of the largest individuals resulted in a substantial loss of live coral cover. For *Acropora*, the size-dependent pattern was less stark, though still significant, with 65% of individuals ≥30-cm diameter having at least 50% partial mortality, compared to 50% of individuals <30-cm diameter. Notably, severe mortality (>50% partial mortality) of juvenile corals (<5 cm diameter) was minimal with <2% of individuals for both *Acropora* and *Pocillopora* experiencing severe partial mortality (Figure 3a,b).

We conducted follow-up surveys in October with a smaller number of corals (Table S1). These data showed that for both *Pocillopora* and *Acropora*, the size-specific patterns in total colony mortality (100% mortality of coral tissue on a colony) closely matched the size-specific patterns of colonies with at least 50% mortality in August (Figure 3a–d). These data suggest that most colonies with severe partial mortality (>50% mortality) in our August surveys had died completely by October.

3.4 | Bleaching reverses past patterns of size-dependent mortality

The pattern of increasing mortality with increasing colony size during the recent marine heatwave reversed the patterns of typical size-structured mortality. Annual surveys tracking the fate of individual *Pocillopora* in permanently marked plots at 10-m depth at four of the six LTER sites (LTER 1, 2, 4, and 5) showed that in years with no or low thermal stress, juvenile corals (<5 cm) had more than twice the annual mortality rate (41%) of corals over 20-cm diameter (18%, Figure 4a). Similarly, for *Acropora*, juvenile corals (<5 cm) had approximately three times the annual mortality rate (32%) of corals over 20 cm (11%, Figure 4b) in years with minimal thermal stress. These patterns of high annual mortality for small corals and low annual mortality for large corals differ dramatically from patterns following the 2019 heatwave where intense thermal stress increased mortality of larger colonies substantially. Thus, in 2018–2019, the relationship between colony size and annual mortality for both genera was significantly different as compared to all other years (GLMM; Size × Year Type interaction $p = .0001$ and $p = .0083$ for *Pocillopora* and *Acropora*, respectively; Figure 4a,b). Therefore, the 2019 thermal stress event eliminated the typical pattern of higher annual survivorship of larger individuals.

3.5 | Estimating effects on coral fecundity

Using our data on the size structure of coral populations from our August 2019 surveys, we estimated fecundity (as the number of eggs produced m^{-2} year^{-1}) for *Pocillopora* and *Acropora* before and after the thermal stress event. To estimate fecundity, we used published relationships between coral size, surface area, and gamete output using a Monte Carlo simulation framework. We found that mortality from the thermal stress event significantly reduced fecundity by 58% and 64% of pre-bleaching levels for *Pocillopora* and *Acropora*, respectively (Figure 5a,c).

Although this event likely decreased fecundity by approximately the same magnitude in the two genera it did so by affecting fecundity differently across size classes. For *Pocillopora*, the bleaching event caused a major shift in the size of individuals responsible for the majority of reproduction due to the loss of the largest individuals (Figure 5b). Prior to the bleaching event, we estimated that individuals ≥30 cm in diameter produced >58% of the total eggs released from *Pocillopora*. However, we estimated that following the bleaching event individuals <30 cm will now be responsible for the majority of reproduction, producing at least 70% of the eggs released by *Pocillopora*. For *Acropora*, the impact on total fecundity was similar to *Pocillopora* but was much less size-specific. In other words, higher overall rates of *Acropora* mortality of individuals large enough to reproduce substantially reduced the total number of eggs released by *Acropora*, but did not result in major changes in the size classes of corals responsible for the majority of reproduction relative to pre-bleaching levels (Figure 5d).

3.6 | Survivorship of coral recruits

In addition to large reductions in fecundity, we also found that survivorship of recently-settled recruits was extremely low during the 2018–2019 marine heatwave. We quantified recruit survivorship using used repeated surveys of removable settlement tiles before and after the thermal stress event. At the first census, each tile had 1–9 recently-settled 1–3 mm coral recruits that were <1-year-old (likely mostly Pocilloporidae with some Acroporidae (Edmunds, 2018), although recruits are notoriously difficult to identify while alive). Mortality of recently-settled coral recruits was extremely high, with 98% of recruits dying between March and July 2019 during the marine heatwave ($n = 34$ tiles, Figure 6a). By comparison, for the same time period in 2017, a year with low thermal stress, only 67% of coral recruits died ($n = 12$ tiles). Thus, survivorship of coral recruits declined by over an order of magnitude, from 33% in 2017, a year with low thermal stress, to 2% in 2019, a year with extreme thermal stress (two-tailed t test, $t = 2.9549$, $df = 11.38$, $p = .0126$, Figure 6a) Applying a more conservative analysis, we asked whether tiles were equally likely to have at least one surviving coral recruit in 2017 and 2019. Our results showed that the likelihood of a tile having at least one surviving coral recruit was an order of magnitude lower in 2019 than in 2017 (6% of tiles vs. 67% of tiles having a surviving coral recruit, respectively; contingency test, $\chi^2 = 15.855$, $df = 1$, $p < .0001$, Figure 6b).

4 | DISCUSSION

Coral bleaching events will likely increase in frequency and intensity as climate change progresses, causing mass-mortalities of corals, the foundation taxa of coral reefs. The prolonged marine heatwave in Moorea, French Polynesia in 2019 resulted in some of the highest levels of thermal stress observed on these reefs for the past 30 years (Leichter et al., 2019; Pratchett et al., 2013; Figure S2). Here, we show that this mass coral bleaching event disproportionately impacted the largest coral colonies. For *Pocillopora*, up to 76% of colonies ≥30-cm diameter died, compared with 17% of individuals <30-cm diameter. For *Acropora*, up to 65% of colonies ≥30-cm diameter died, compared to 50% of individuals <30-cm diameter. In other words, colonies of *Pocillopora* and *Acropora* ≥30-cm diameter were ~3.5× and ~1.3×, respectively, more likely to die than colonies <30-cm diameter. This event reshaped typical size-mortality patterns, where smaller corals are more likely to die in a given year, and eliminated the major reproducers of two dominant coral taxa. Because large coral colonies are very fecund and disproportionately responsible for reproduction on coral reefs (Hall & Hughes, 1996), we estimate that this bleaching event reduced overall fecundity on these reefs by >58% for both *Pocillopora* and *Acropora*. Further, we show that 98% of coral recruits died during this heatwave, an order of magnitude decrease in survivorship as compared to years without thermal stress. Together, these results suggest that bleaching events may compromise the recovery capacity of coral reefs by disproportionately impacting the life stages most critical for reef recovery, coral recruits, and the largest, most fecund corals.

4.1 | Impacts of marine heatwaves on the largest corals

Morphological and taxonomic differences in susceptibility to thermal stress drive variability in coral bleaching and mortality (Loya et al., 2001). This idea of "winners and losers" among taxa in coral communities in response to heat stress is well known (Marshall & Baird, 2000; van Woesik et al., 2011), where branching and plating taxa tend to bleach and die more frequently than massive and encrusting taxa (Loya et al., 2001). However, we show that even within taxa there are "winners and losers" as colony size also drives major variability in response to thermal stress within taxa. We showed that larger colonies of *Pocillopora* spp. and *Acropora* spp. are significantly more likely to die from bleaching compared with smaller conspecifics. Past work has shown that juvenile corals are relatively resistant to bleaching compared to adults (Bena & Van Woesik, 2004; Depczynski et al., 2013; Loya et al., 2001), and small-scale field studies have found that coral colony size can be positively correlated with bleaching prevalence, severity, and mortality (Bena & Van Woesik, 2004; Depczynski et al., 2013; Pratchett et al., 2013; Shenkar et al., 2005). Here, we show that these relationships can manifest in landscape-scale patterns of coral mortality following a severe marine heatwave.

Although it was not the aim of our study to evaluate the mechanisms that drove size-dependent bleaching, it is likely that several mechanisms, which are not mutually exclusive, contributed to the size-dependent patterns of bleaching susceptibility and mortality. First, strong theoretical and empirical evidence suggests that differences in mass transfer rates can make larger corals more susceptible to bleaching during thermal stress (Nakamura & Woesik, 2001; van Woesik et al., 2012). One mechanism of coral bleaching is when harmful metabolites (oxygen radicals) produced by coral photosymbionts build up in coral tissues during periods of thermal stress (Downs et al., 2002; Lesser et al., 1990). Mass transfer rates govern corals' ability to exchange metabolites with the surrounding seawater, and these rates vary with size and morphology for marine invertebrates (Bena & Van Woesik, 2004; Nakamura & Woesik, 2001; Patterson, 1992; van Woesik et al., 2012). Therefore, due to lower mass transfer rates, larger coral colonies may be less likely to shed these harmful metabolites formed during thermal stress, resulting in more severe bleaching and mortality (van Woesik et al., 2012). Additionally, smaller corals are often relatively flat and have a low height to diameter ratio compared to larger, highly branched colonies of the same taxa. Flatter morphologies typically have higher rates of mass transfer than branching morphologies, and this could contribute to higher bleaching resistance in smaller corals (Loya et al., 2001). It is also possible that ontogenetic differences in Symbiodiniaceae communities (Coffroth et al., 2001; McIlroy et al., 2019) or efficiency of photosynthetic pathways (Edmunds & Gates, 2004) make smaller corals more resistant to thermal stress.

Another mechanism that likely contributed to size-dependent bleaching is differential bleaching susceptibility among cryptic species of *Pocillopora* (Burgess et al., 2021). Corals in the genus *Pocillopora* exhibit significant phenotypic plasticity with many species being morphologically indistinguishable in the field (Johnston et al., 2017). Molecular identification of *Pocillopora* corals in Moorea suggests that at the time of the bleaching event, large individuals may have been disproportionately represented by thermally sensitive cryptic species that experienced higher rates of mortality than other cryptic species (Burgess et al., 2021). Differences in thermal sensitivity among cryptic species of *Pocillopora* likely played a role in driving the size-dependent bleaching and mortality during this event (Burgess et al., 2021). Size-dependent bleaching may have also occurred within *Pocillopora* species, and this pattern has been reported for several species in other genera (Brandt, 2009; Shenkar et al., 2005). Several of these mechanisms are likely operating in concert to drive the size-dependent patterns in morality we saw where the largest individuals of the two dominant genera were nearly completely extirpated.

It is possible that the patterns we observed were driven in part by mass coral settlement events following past disturbances in Moorea. From 2007 to 2009, the reefs around Moorea experienced a severe COTS outbreak followed by a cyclone in 2010 that resulted in the landscape-scale loss of nearly all corals on the outer reef (Adam et al., 2011; Kayal et al., 2011). Following these disturbances, Moorea's reefs returned to pre-disturbance coral cover in less than a decade, which was largely driven by high rates of coral recruitment (Holbrook et al., 2018). These catastrophic disturbances from 2007 to 2010 removed the existing population size structure and genetic diversity, and recovery was likely driven by the establishment and success of just a few cohorts of new individuals that grew to reach large size classes at the same time. If the coral size is a strong driver of variation in bleaching susceptibility, as our data shows, then reefs that were dominated by large individuals, especially if they were of bleaching-sensitive cryptic species, would have been particularly vulnerable to marine heatwaves that could cause another mass-mortality event. Furthermore, bleaching events that eliminate entire size classes of large individuals may set the stage for sequential catastrophic disturbances from bleaching as cohorts of corals that are relatively uniform in size grow into the bleaching-sensitive size class at the same time.

4.2 | Vulnerability of coral recruits to thermal stress

Coral recruitment is an essential first step for the recovery of coral populations following catastrophic disturbances, and processes that inhibit recruitment or recruit survival can create bottlenecks that slow or prevent coral recovery. Low rates of recruitment are common following severe bleaching events (Aronson et al., 2002; Burt & Bauman, 2020; Roth et al., 2010), and past work has suggested that this is driven by the breakdown of stock-recruitment relationships due to the loss of reproductive adults (Hughes et al., 2019). However, it is also possible that recruits are scarce after bleaching events if recruits already present on the benthos have high rates of mortality during periods of thermal stress. Our data are the first to suggest that the paucity of coral recruits following bleaching events may be influenced by near-complete loss of entire cohorts of newly settled coral recruits in addition to loss of the largest, most fecund corals during these events. To our knowledge, this is the first published data on survivorship of coral recruits in situ during a marine heatwave.

Coral recruits have high rates of early post-settlement mortality because they are highly vulnerable to predation (Christiansen et al., 2009; Gallagher & Doropoulos, 2017), competition (Arnold & Steneck, 2011), and stressors such as sedimentation and pollution (Babcock & Smith, 2002; Negri et al., 2005). Limited data from laboratory experiments (Fourney & Figueiredo, 2017; Nozawa & Harrison, 2007) and our unique data from *in situ* recruits show that marine heatwaves may also be a significant source of post-settlement mortality. Why coral recruits experience such high mortality during thermal stress (98% in our study) is uncertain. Many coral recruits of broadcast spawning corals (which typically account for >90% of recruits in Moorea; Edmunds, 2018) begin life as aposymbiotic larvae that acquire symbionts from the environment (horizontal transmission) as larvae or early after settlement. Some evidence suggests that depriving coral recruits of symbionts in the first ~7 months post-settlement can substantially reduce their propensity to acquire symbionts later (McIlroy & Coffroth, 2017). It is possible that severe thermal stress that occurs early in ontogeny for coral recruits impairs the ability of recruits to acquire symbionts, which would adversely affect survival. Other work has shown that the respiration rate of coral recruits increases substantially at higher temperatures, suggesting that as temperatures increase coral recruits will have higher metabolic rates and, therefore, will require more energy to meet their metabolic needs (Edmunds, 2005). In the context of a prolonged marine heatwave, higher energy demands may be detrimental to coral recruits, especially if recruits have low densities of symbionts and therefore are receiving less photosynthetically derived energy. Regardless of the mechanisms, high rates of mortality in coral recruits during marine heatwaves will have far-reaching consequences for coral population dynamics and will probably slow coral recovery following bleaching events and other climate-driven perturbations.

4.3 | Consequences for coral reproduction

Corals are modular, colonial organisms that become reproductively mature once they reach a size threshold, beyond which fecundity increases with colony size (Hall & Hughes, 1996). Size-specific fecundity makes large, mature colonies disproportionality important for reproduction. We showed that large colonies were also the most likely to die during the 2019 bleaching event, and we estimated that the size-specific patterns in mortality that we documented will reduce fecundity by >60% for *Pocillopora* spp. and *Acropora* spp. on these reefs (Figure 5). This major reduction in the abundance of reproductive corals, and the near-complete extirpation of large colonies will greatly reduce the number of coral larvae produced. Fewer larvae could slow reef recovery, especially if most of the larvae available to these reefs are self-seeded as opposed to arriving from other sources, which may be the case for *Pocillopora* on reefs around Moorea (Edmunds et al., 2016).

When large colonies are lost to bleaching there will be a major shift in the reproductive burden from large to small colonies, and this will likely have more severe effects on fecundity that our estimates did not capture. For example, larger colonies can produce larger eggs per polyp, therefore, giving offspring more stored energy and a better chance of survival, than smaller conspecifics (Baird & Marshall, 2002), a relationship that we did not account for in our estimates of fecundity. Additionally, the sex allocation (volume of eggs and sperm produced) of corals can vary substantially with colony size, where larger colonies invest more energy in producing eggs (Hall & Hughes, 1996). Thus, truncating the size distribution of corals may result in a higher ratio of sperm to eggs produced by the remaining corals. The energetic costs associated with bleaching stress and recovery can also cause the surviving corals to reduce (Fine et al., 2001) or stop gamete production (Szmant & Gassman, 1990) for years following bleaching events (Levitan et al., 2014). Thus, this bleaching event will likely have substantially more negative effects on fecundity than we estimate, likely creating a substantial bottleneck to coral recovery. If the size-dependent bleaching mortality that we observed in Moorea is a widespread pattern, dampening of fecundity caused by the loss of large individuals will be a significant impact to the resilience of coral reefs worldwide.

One challenge for our study was that we necessarily had to analyze our data at the genus level due to the inability to differentiate cryptic species in the field and the challenge in identifying recently dead, algal-covered corals past genus level. While grouping taxa at the genus level is not ideal, it is commonly done across the coral literature (as well as in other systems where visual taxonomy is challenging) because understanding patterns of mortality at the genus level is often ecologically meaningful for understanding the community and landscape-scale consequences of coral bleaching events. Loss of the largest corals, regardless of the species, will result in a substantial decrease in the number of coral larvae produced by the coral community, and, therefore, significantly fewer larvae will be available to reseed the reef.

4.4 | Cascading impacts of losing the largest corals

The loss of the largest corals and subsequent shifts to the higher relative abundance of smaller individuals will drastically alter the reefscape, likely triggering cascading impacts on other reef taxa that rely on corals for habitat (Hughes et al., 2018). Immediately following bleaching events, the loss of live coral cover can cause substantial declines in fishes and invertebrates that rely directly on live coral for food and shelter (Wilson et al., 2006). The loss of structural complexity, a long-term consequence of bleaching-induced coral mortality, can also trigger severe declines in fish and invertebrate abundance and diversity beyond those taxa that directly rely on corals (Adam et al., 2014; Pratchett et al., 2008). Corals create structural complexity that moderates competition and predation among reef inhabitants, and as it is lost, fish abundance, diversity, and functional redundancy also decline (Pratchett et al., 2008, 2011). Large corals are disproportionately important for the provisioning of habitat for reef inhabitants (Abele & Patton, 1976), therefore, the loss of the largest corals during a marine heatwave will likely result in the reorganization of fish and invertebrate communities that could not be predicted based on the magnitude of loss in coral abundance alone.

In summary, our study reveals that a marine heatwave not only caused mass coral bleaching and mortality, but that it reversed typical size-mortality relationships, causing near-complete loss of the largest individuals of the dominant taxa. As marine heatwaves and coral bleaching events become more frequent and intense, they may truncate the size distribution of bleaching-sensitive coral taxa, resulting in persistent shifts in coral population size structure skewed toward small individuals. Importantly, the asymmetric loss of large individuals can have more adverse effects on the persistence of populations than does the loss of juveniles or earlier life stages (Edmunds & Elahi, 2007; Heppell et al., 1996; Hixon et al., 2014; Vardi et al., 2012). Large corals, which typically have low mortality rates and high fecundity rates, are disproportionately important for seeding reef recovery and for creating habitat structure for other taxa.

The higher sensitivity of large corals to bleaching-induced mortality parallels the disproportionate loss of other large foundation species, like trees during droughts. Large trees, like large corals, may be more sensitive to the effects of climate change because they are more likely to experience severe changes in physiological processes during extreme events (Rowland et al., 2015). The disproportionate loss of large, ecologically important individuals of foundation taxa due to climate change will have cascading impacts on ecosystems. By fundamentally reshaping typical demographic patterns, climate change-driven disturbances may slow recovery rates of foundation species, ultimately reorganizing the assemblages that depend on them for habitat.

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CONFLICT OF INTEREST

The authors declare that they have no competing interests.

AUTHOR CONTRIBUTIONS

All authors designed the study and collected data. Kelly E. Speare and Thomas C. Adam analyzed the data. Kelly E. Speare wrote the first draft of the manuscript, and all authors contributed to editing.

DATA AVAILABILITY STATEMENT

Water temperature data are available at https://doi.org/10.6073/pasta/ea6a89415b1d9118d441235723c1a23f, benthic survey data are available at https://doi.org/10.6073/pasta/f59968d039de006909c5c92c51c3919c, demographic survey data are available at https://doi.org/10.6073/pasta/92e72c8c91056f4d89a11a1b67b2c373, and coral recruit survival data are available at https://doi.org/10.6073/pasta/f59968d039de006909c5c92c51c3919c.

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