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Divergent bleaching and recovery trajectories in reef-building corals following a decade of successive marine heatwaves

Kristen T. Brown[a] 📍, Elizabeth A. Lenz[b], Benjamin H. Glass[a] 📍, Elisa Kruse[a] 📍, Rayna McClintock[c], Crawford Drury[d] 📍, Craig E. Nelson[b,c] 📍, Hollie M. Putnam[e] 📍, and Katie L. Barott[a,1] 📍

Increasingly frequent marine heatwaves are devastating coral reefs. Corals that survive these extreme events must rapidly recover if they are to withstand subsequent events, and long-term survival in the face of rising ocean temperatures may hinge on recovery capacity and acclimatory gains in heat tolerance over an individual's lifespan. To better understand coral recovery trajectories in the face of successive marine heatwaves, we monitored the responses of bleaching-susceptible and bleaching-resistant individuals of two dominant coral species in Hawai'i, *Montipora capitata* and *Porites compressa*, over a decade that included three marine heatwaves. Bleaching-susceptible colonies of *P. compressa* exhibited beneficial acclimatization to heat stress (i.e., less bleaching) following repeat heatwaves, becoming indistinguishable from bleaching-resistant conspecifics during the third heatwave. In contrast, bleaching-susceptible *M. capitata* repeatedly bleached during all successive heatwaves and exhibited seasonal bleaching and substantial mortality for up to 3 y following the third heatwave. Encouragingly, bleaching-resistant individuals of both species remained pigmented across the entire time series; however, pigmentation did not necessarily indicate physiological resilience. Specifically, *M. capitata* displayed incremental yet only partial recovery of symbiont density and tissue biomass across both bleaching phenotypes up to 35 mo following the third heatwave as well as considerable partial mortality. Conversely, *P. compressa* appeared to recover across most physiological metrics within 2 y and experienced little to no mortality. Ultimately, these results indicate that even some visually robust, bleaching-resistant corals can carry the cost of recurring heatwaves over multiple years, leading to divergent recovery trajectories that may erode coral reef resilience in the Anthropocene.

climate change | ocean warming | coral bleaching | environmental memory | acclimatization

Ocean warming driven by climate change has led to staggering losses of live coral on coral reefs worldwide and is among the most pressing of stressors threatening the survival of coral reefs today (1, 2). As mean ocean surface temperatures have steadily increased, there has been a corresponding increase in the occurrence of marine heatwaves (3, 4). These extreme warm water events can persist for days to months, frequently leading to coral bleaching, a symptom of the breakdown of the symbiosis between corals and their dinoflagellate algal endosymbionts (family Symbiodiniaceae) (5). This symbiosis is the energetic foundation of coral reef ecosystems, allowing for high rates of productivity in otherwise oligotrophic seas (6). The energy corals receive from symbiont photosynthesis supports a majority of their metabolic demand (7), thus fueling the construction of the complex three-dimensional framework necessary to support the most biodiverse ecosystems in the ocean (8). Given this significance, the breakdown of the coral–algal symbiosis during coral bleaching can have devastating consequences for coral reef ecosystems, ranging from declines in primary production to widespread coral mortality and reef erosion (1, 9). These losses can lead to concomitant declines in biodiversity and ecosystem function that harm not just these ecosystems but also the human societies that rely on the myriad services functioning coral reefs provide (10). As marine heatwaves become increasingly frequent and severe (11), coral bleaching events are predicted to correspondingly increase (12). However, the extent to which individual corals can acclimatize to these conditions within their lifetime and thus gain resistance to recurring marine heatwaves remains a critical outstanding question.

Environmental memory of thermal stress, defined as the retention of information from an initial exposure that modifies the response to a later exposure, has been posited to lead to beneficial acclimatization of individuals exposed to repeat marine heatwaves (13–16). Indeed, coral communities that experienced sublethal heat stress and/or bleaching during marine heatwaves were less prone to bleaching in subsequent exposures across the Caribbean (17, 18), Great Barrier Reef (19), and Indo-Pacific (15, 16, 20, 21). There are

Significance

Coral reefs are in jeopardy as climate change leads to increasingly frequent marine heatwaves. Some corals survive these extreme events, and this exposure may prime corals to increase their heat tolerance. Yet, as the time between heatwaves decreases, the accumulation of stress experienced may preclude opportunities for beneficial gains in heat tolerance. This nearly decade-long study revealed that repetitive exposure to heatwaves leads to divergent coral bleaching and recovery trajectories. Some corals increased bleaching resistance and demonstrated physiological recovery, whereas others exhibited alarming seasonal bleaching and accumulating mortality without heat stress following successive heatwaves. As the climate continues to change, surviving corals must not only gain heat tolerance but also rapidly recover to maintain critical ecosystem services that humans rely on.

likely multiple factors driving these increases in coral community heat tolerance, including beneficial acclimatization of surviving individuals (e.g., epigenetic modifications) (13–15), shifts in community composition driven by losses of bleaching-susceptible individuals (19, 22–25), and selection for thermally tolerant offspring (i.e., adaptation) (26). However, exposure to sublethal heat stress in individual corals may not always lead to benefits in subsequent exposures (27), as a history of heat stress could exacerbate the effects of subsequent heat stress (i.e., sensitization) when corals have not fully recovered (28–30). In light of the increasing frequency and severity of marine heatwaves (11), there is a growing need to better understand how individual corals are responding to and recovering from repeat heatwaves and the ecological consequences of environmental memory for reef resilience into the future. Encouragingly, phenotypic diversity in bleaching susceptibility varies both within and between coral species, which is likely an important source of adaptive variation (31) that could lead to directional selection of bleaching resistance (e.g., ref. 20). However, the pace of ocean warming requires rapid acclimatization of established adult colonies in order to buy time for adaptation and proliferation of the next generation of thermally tolerant corals, which may take several decades to centuries in these long-lived and slow-growing species (32). As marine heatwaves have only recently begun occurring on multidecadal time scales (1), we are just beginning to understand the capacity for individuals to recover, acclimatize, or sensitize following heat stress (14). Further, understanding how phenotypic variation in these responses between individuals and species influences population dynamics in the field remains underexplored, yet has important implications for predicting ecosystem diversity and function in the face of a rapidly changing climate (5).

In order to address this critical gap in our knowledge, we examined the responses of coral communities and individual colonies of two dominant reef-building coral species in Hawai'i, *Montipora capitata* and *Porites compressa,* throughout a decade that included three marine heatwaves (2014, 2015, and 2019). Adjacent conspecific colonies with contrasting bleaching phenotypes (i.e., bleaching-resistant vs. bleaching-susceptible) were first identified in 2015 during the second of two consecutive coral bleaching events that occurred in Kāne'ohe Bay in 2014 and 2015 (33). Individual coral pigmentation, cumulative colony mortality, and reef-wide bleaching prevalence were tracked across the next 9 y (2015 to 2023), which included another bleaching event in 2019 (34). Following the 2019 event, we repeatedly assessed a suite of physiological parameters (e.g., metabolic rates, symbiont densities, host biomass and tissue composition) over 3 y to better understand intra- and interspecific variation in individual colony recovery trajectories following repeat heat stress. In addition, we explored the capacity for environmental memory to influence coral thermotolerance through a standardized short-term heat stress assay of these same individuals (35). This nearly decade-long investigation of individual coral colonies that encompass the phenotypic extremes within populations of these two species in the field is a powerful framework to test the hypothesis that divergent responses to repeat in situ heat stress lead to variation in recovery trajectories, with consequences for future heat tolerance and coral reef survival.

Results

Three Successive Heatwaves Influenced Reef-Wide Coral Bleaching Prevalence. Between 2014 and 2023, three significant thermal anomalies were documented across Kāne'ohe Bay (Fig. 1 and *SI Appendix*, Figs. S1 and S2 and Tables S1 and S2). During these events, maximum sustained degree heating weeks (DHW) at Patch Reef 13 (PR13) were lower in 2014 (7.3 °C wk^{-1}) than 2015 (8.8 °C wk^{-1}) and lowest in 2019 (5.1 °C wk^{-1}) (Fig. 1 and *SI Appendix*, Tables S1 and S2). In contrast, 2019 was the most severe of the three events in the southern end of the bay and regionally (10 to 14 °C wk^{-1}; *SI Appendix*, Table S2). From 2015 to 2023, coral cover at PR13 was dominated by *P. compressa* (53.5% ± 0.9) and *M. capitata* (12.5% ± 0.5) (*SI Appendix*, Fig. S3). At the peak of the 2015 heatwave, reef-wide bleaching prevalence reached 39.1% for *M. capitata* and 44.9% *P. compressa*, declining 2 mo after the heatwave in *P. compressa* (1.4%), but not *M. capitata* (35.5%) (*SI Appendix*, Fig. S4). The following summer, bleaching prevalence across PR13 reached 38.1% for *M. capitata* in the absence of any measurable heat stress but was rarely observed for *P. compressa* (0.2%) (Fig. 2). This cyclic seasonal pattern of decreased bleaching prevalence of *M. capitata* in winter and increased bleaching prevalence in summer continued the following year. At the peak of the 2019 heatwave, reef-wide bleaching prevalence increased to similar levels observed in the 2015 heatwave in both *M. capitata* (45.9%) and *P. compressa* (38.8%) (*SI Appendix*, Fig. S4); however, despite similar prevalence, the severity of bleaching was threefold lower for *P. compressa* in 2019 than 2015 (34). Notably, bleaching prevalence again showed a cyclic seasonal pattern in *M. capitata*, declining in winter and increasing in each of the three summers following 2019 (September 2020: 46.9%; October 2021: 21.7%; September 2022: 14.9%). In contrast, reef-wide bleaching prevalence of *P. compressa* did not change between seasons and remained low (0.7 to 3.2%) (*SI Appendix*, Fig. S4).
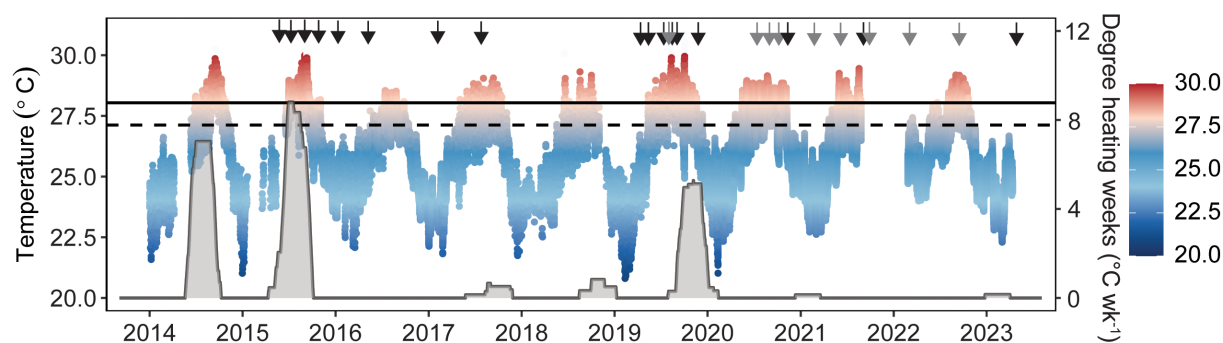
Fig. 1. Temperature profile and heat stress accumulation over time. In situ temperatures were recorded from January 2014 to April 2023 at a depth of 0.7 to 2.7 m in Kāne'ohe Bay. Points indicate hourly measurements (metadata in *SI Appendix*, Table S1). Heat stress accumulation was estimated by DHW (gray shading) calculated from mean daily (24 h) temperatures. Black arrows indicate image collection, and gray arrows indicate image collection with physiological sampling. The dashed horizontal line indicates the Kāne'ohe Bay's climatological maximum monthly mean (MMM; 27.3 °C), and the solid horizontal line indicates the local coral bleaching threshold (MMM + 1 °C; 28.3 °C).
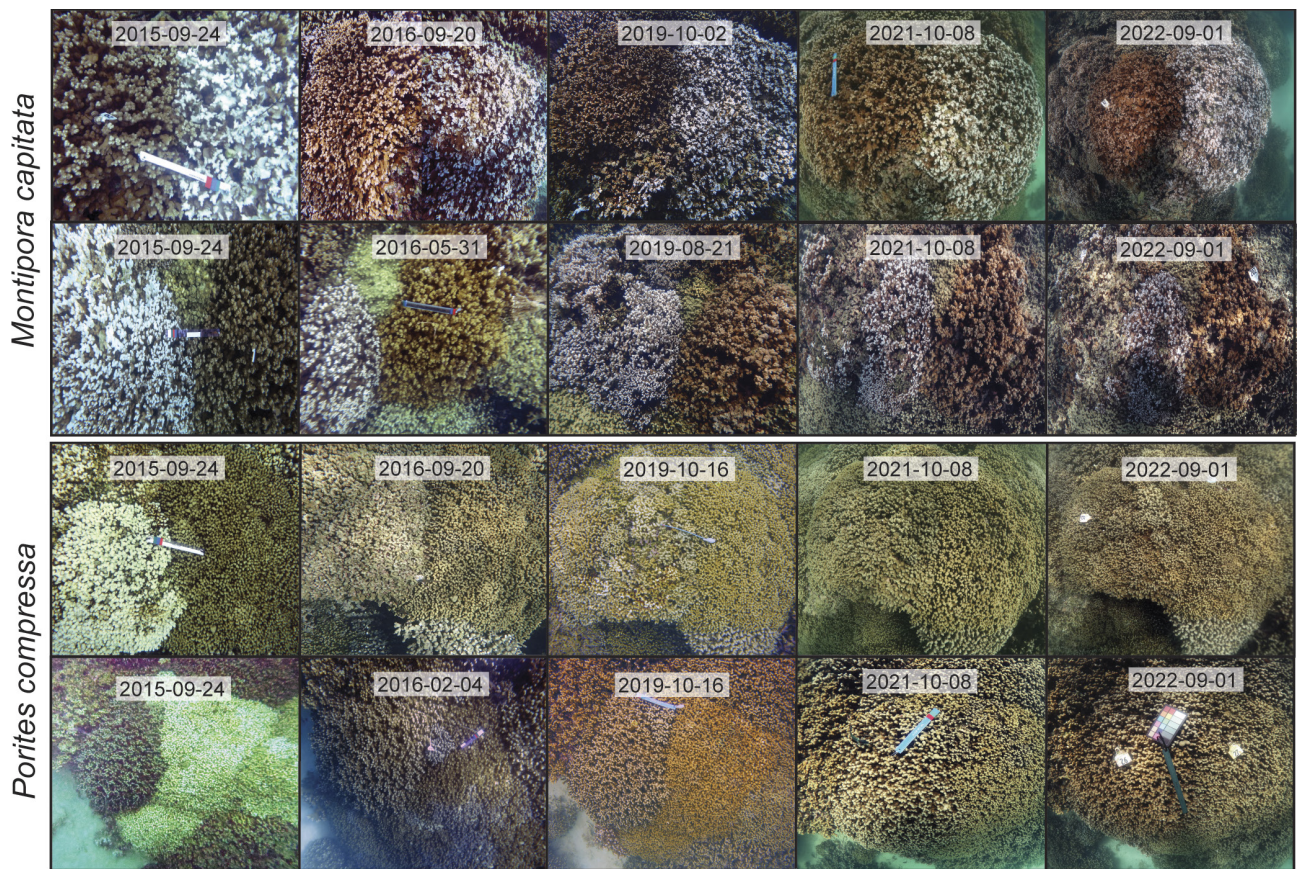
Fig. 2. Representative images of *M. capitata* and *P. compressa* pairs over time in Kāne'ohe Bay. Each row depicts a single pair of bleaching-susceptible and bleaching-resistant individuals from 2015 to 2022 (the *Inset* indicates the date the image was taken), and the corals appear in the same orientation in each image within each row.

Acclimatization and Sensitization in Colony Phenotypes across Recurring Heatwaves. Colony-level bleaching severity was tracked across the same individuals (*SI Appendix*, Tables S3 and S4 and Figs. S5 and S6) and was influenced by the significant four-way interaction between coral species, phenotype, season (i.e., winter vs. summer), and time (F = 6.12, $P < 0.0001$) (*SI Appendix*, Table S5). During the 2015 heatwave, bleaching-susceptible *M. capitata* and *P. compressa* underwent the greatest bleaching (e.g., 100% bleached), whereas bleaching-resistant conspecifics remained fully pigmented ($P < 0.0001$) (Figs. 2 and 3). Throughout the next 2 y (2016 to 2017), bleaching-susceptible *M. capitata* remained half as pigmented as bleaching-resistant conspecifics regardless of season ($P \le 0.04$) (Figs. 2 and 3). Interestingly, *P. compressa* phenotypes were indistinguishable by the summer after the heatwave ($P = 0.23$), and remained so throughout 2017 (Figs. 2 and 3). During the 2019 marine heatwave, bleaching-susceptible *P. compressa* ($P < 0.03$) and bleaching-susceptible *M. capitata* ($P < 0.0001$) were again less pigmented than bleaching-resistant conspecifics. Compared to the previous 2015 heatwave when all susceptible individuals were severely bleached, bleaching-susceptible *M. capitata* were moderately bleached (30% less severe) during the 2019 heatwave, whereas bleaching-susceptible *P. compressa* were only mildly affected (Figs. 2 and 3). For the next 2 y (2020 to 2021), bleaching-susceptible *M. capitata* remained half as pigmented than bleaching-resistant conspecifics regardless of season ($P < 0.0001$), whereas *P. compressa* phenotypes were indistinguishable by winter 2020 and remained so throughout 2021 to 2023 ($P > 0.49$) (Figs. 2 and 3). By winter 2022, *M. capitata* phenotypes were indistinguishable for the first time during the study period following the initial bleaching ($P = 0.5$), yet in

the subsequent summer, bleaching-susceptible *M. capitata* were again less pigmented than bleaching-resistant phenotypes ($P < 0.0001$) (Figs. 2 and 3).

Colony-level partial mortality was influenced by the significant interaction between species and time ($\chi^2 = 86.9$, $P < 0.0001$) (*SI Appendix*, Table S6). Following the 2015 marine heatwave, there were no detectable differences in partial mortality between *M. capitata* and *P. compressa* ($P > 0.42$) (Figs. 2 and 3); however, bleaching-susceptible individuals of both *M. capitata* (14%) and *P. compressa* (21%) exhibited significantly greater partial mortality than bleaching-resistant conspecifics (0% for *M. capitata*, 2% for *P. compressa*) in the first 2 y following that heatwave (Figs. 2 and 3; 33). In the first 6 mo following the 2019 heatwave, *M. capitata* exhibited significantly greater partial mortality across both bleaching-susceptible (20%) and bleaching-resistant (31%) individuals than *P. compressa* (<10% for both phenotypes) ($P < 0.03$) (Figs. 2 and 3). In the 3 y after the 2019 heatwave (2020 to 2023), *M. capitata* partial mortality steadily increased across both bleaching-susceptible (up to 56%) and bleaching-resistant (up to 47%) individuals, while *P. compressa* remained low (<5%). From the 2019 heatwave onward, there were no significant differences of phenotype, interactive or otherwise ($\chi^2 = 20.7$, $P = 0.11$).

Intra- and Interspecific Trajectories in Physiological Metrics Indicate Prolonged and Incomplete Recovery. Coral physiological parameters were assessed from October 2019 (during the marine heatwave) to September 2022 (35 mo post heat stress) (Fig. 4 and *SI Appendix*, Fig. S7 and Table S7). Host tissue biomass ($\chi^2 = 15.9$, $P < 0.03$) and host lipid densities ($\chi^2 = 25.2$, $P < 0.0003$) were
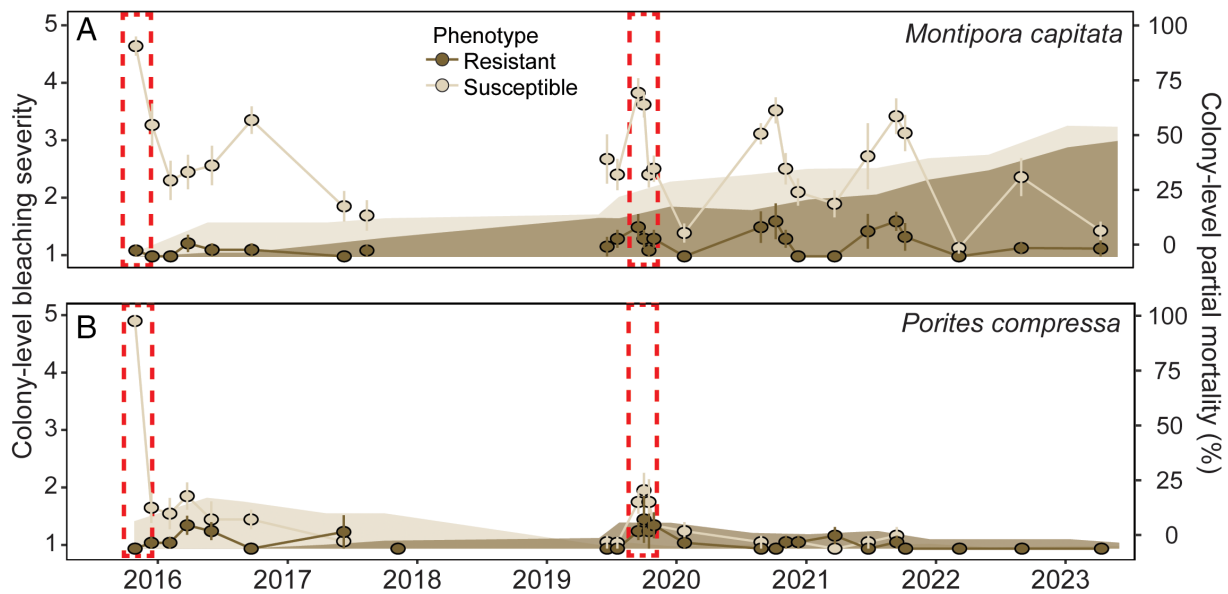
Fig. 3. Bleaching and mortality response of individual bleaching-resistant and bleaching-susceptible corals over time. Colony-level bleaching severity (solid lines; mean ± SE) and cumulative colony-level partial morality (shading; mean) from September 2015 to April 2023 for individual colonies of (*A*) *M. capitata* (n = 9 to 10) and (*B*) *P. compressa* (n = 7 to 10). Colony-level bleaching severity was visually determined for each colony following the methodology of ref. 34, where (1) represents 0% bleached and (5) >80% bleached. Dashed red rectangles indicate the 2015 and 2019 marine heatwaves.

significantly influenced by the interaction between coral species and time (Fig. 4) (*SI Appendix*, Table S8). Specifically, *P. compressa* had 20 to 90% greater host tissue biomass than *M. capitata* across the time series (*P* < 0.003), with biomass converging 3 y after the 2019 marine heatwave (*P* = 0.24) (Fig. 4*A* and *SI Appendix*, Fig. S7). For both *M. capitata* and *P. compressa*, tissue biomass and lipid densities displayed strong seasonality, where tissue parameters were greatest March–June prior to annual coral spawning (Fig. 4). During seasonal temperature maxima, tissue biomass for both coral species did not differ from the 2019 marine heatwave in the first summer following the heatwave (2020, *P* > 0.44), although biomass eventually increased by 95% in the second summer (2021, *P* < 0.0008) and 163% by the third summer (2022, *P* < 0.0001) (*SI Appendix*, Fig. S7).
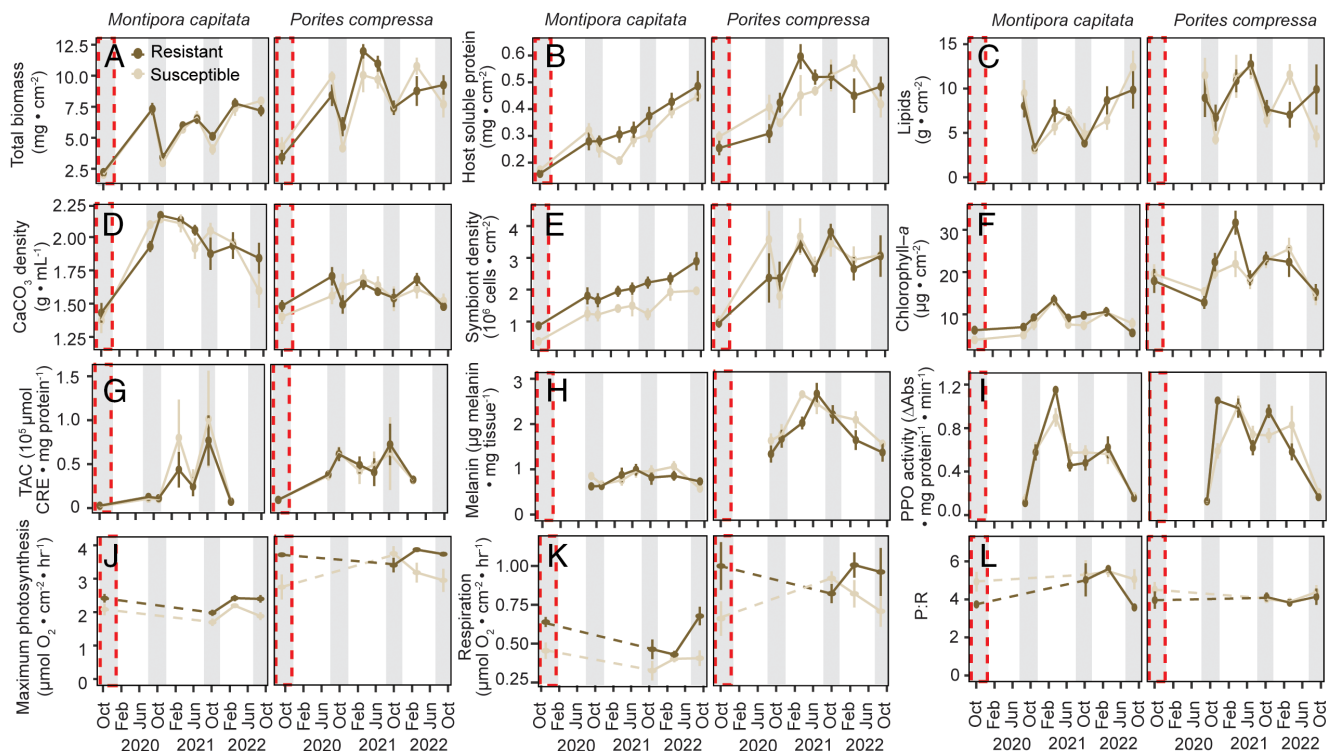
Fig. 4. Physiological response of bleaching-resistant and bleaching-susceptible corals over time. (*A*) Host total tissue biomass (ash-free dry weight), (*B*) host soluble protein density, (*C*) host lipid density, (*D*) calcium carbonate (CaCO₃) density, (*E*) endosymbiont cell density, (*F*) chlorophyll-*a* concentration, (*G*) host total antioxidant capacity (TAC), (*H*) host melanin content, (*I*) host prophenoloxidase (PPO) activity, (*J*) maximum photosynthetic rates, (*K*) light-enhanced dark respiration rates, and (*L*) photosynthesis to respiration ratios (P:R) for bleaching-susceptible and bleaching-resistant *M. capitata* and *P. compressa*. Points and error represent the mean ± SE (n = 4 to 10). The gray shading indicates seasonal peak temperatures (i.e., September–October), with a dashed red rectangle representing the 2019 marine heatwave.

Host soluble protein density was significantly influenced by the interaction between coral species and time (χ^2 = 20.5, $P < 0.004$) (*SI Appendix,* Table S8). Generally, *P. compressa* tissues had ~40% greater protein concentration than *M. capitata* across the time series ($P < 0.008$), apart from 10 mo post heat stress ($P = 0.1$), and later with protein concentration of the two species converging 3 y after the 2019 marine heatwave (2022; $P = 0.55$) (Fig. 4*B*). For *M. capitata*, protein concentration showed a stepwise increase over time, with concentration significantly greater across all time points when compared to the 2019 marine heatwave ($P < 0.05$). While bleaching-susceptible *M. capitata* protein concentration trended lower than bleaching-resistant conspecifics, there was no significant influence of phenotype (χ^2 = 0.11, $P = 0.74$). For *P. compressa*, there was no detectable difference in protein concentration between the 2019 marine heatwave and 10 mo post heat stress ($P = 0.16$), yet by 13 mo, protein concentration was significantly greater (40 to 89%) across all subsequent time points ($P < 0.01$) (Fig. 4*B* and *SI Appendix,* Fig. S7). Interestingly, during seasonal temperature maxima, *P. compressa* protein concentration was 35% lower 13 mo post heat stress than 24 mo ($P = 0.003$), yet there were no observable differences between 24 and 35 mo ($P = 0.46$) (*SI Appendix,* Fig. S7).

Calcium carbonate ($CaCO_3$) bulk density was significantly influenced by the three-way interaction between coral species, phenotype, and time (χ^2 = 14.1, $P = 0.05$) (*SI Appendix,* Table S6). During the 2019 marine heatwave, $CaCO_3$ density declined by up to 50% for *M. capitata* and up to 14% for *P. compressa* regardless of phenotype, at which time density was indistinguishable between coral species ($P > 0.72$) (Fig. 4*D* and *SI Appendix,* Fig. S7). Across the rest of the time series, $CaCO_3$ density was nearly 20% greater in *M. capitata* when compared to *P. compressa* regardless of phenotype ($P < 0.05$), with the exception of bleaching-susceptible corals at 35 mo post heat stress ($P = 0.52$). For bleaching-resistant *M. capitata*, however, $CaCO_3$ density was up to 55% greater across all time points when compared to the 2019 heatwave ($P < 0.002$) (Fig. 4). For bleaching-susceptible *M. capitata*, $CaCO_3$ density was also significantly greater across all time points when compared to the 2019 heatwave (32 to 47%) ($P < 0.0001$), with the exception of 35 mo postheat stress when $CaCO_3$ density was depressed (5% lower than 29 mo post heat stress) ($P = 0.59$) (Fig. 4*D*). Although bleaching-susceptible *P. compressa* trended lower than bleaching-resistant conspecifics during and 10 mo after the marine heatwave, pairwise comparisons revealed that, for *P. compressa* of either phenotype, $CaCO_3$ density was not significantly different across time ($P > 0.05$) (Fig. 4*D* and *SI Appendix,* Fig. S7).

Symbiont densities were significantly influenced by the interaction between coral species and time (χ^2 = 16.4, $P = 0.02$) (*SI Appendix,* Table S8). While bleaching-susceptible *M. capitata* symbiont densities were approximately 50% lower than bleaching-resistant conspecifics across the study, the influence of phenotype was not statistically significant (χ^2 = 1.15, $P = 0.28$) (Fig. 4*E* and *SI Appendix,* Fig. S7). Pairwise comparisons revealed that, generally, *P. compressa* had ~60% greater symbiont densities than *M. capitata*, apart from during the 2019 heatwave when both species experienced declines ($P = 0.25$), and at 29 and 35 mo post heat stress ($P > 0.07$), when symbiont densities were greatest (Fig. 4*E* and *SI Appendix,* Fig. S7). For *M. capitata*, symbiont densities did not rebound immediately after the 2019 heatwave, and were indistinguishable from the 2019 heatwave until 17 mo post heat stress, after which symbiont densities increased by 200% by 2023. In contrast, *P. compressa* symbiont densities were significantly greater across all time points when compared to the 2019 marine heatwave (~175 to 260%) ($P < 0.02$) and indicated seasonal patterns (Fig. 4*E*). For *P. compressa*, symbiont densities were

significantly higher 24 mo post heat stress than 13 mo ($P = 0.0005$), yet there was no significant difference between 24 and 35 mo ($P = 0.74$) (*SI Appendix,* Fig. S7).

Chlorophyll-*a* content was significantly influenced by the three-way interaction between coral species, phenotype, and time (χ^2 = 14.9, $P = 0.04$) (*SI Appendix,* Table S8). Pairwise comparison revealed only one significant difference between bleaching-susceptible or bleaching-resistant phenotypes; that is, in March 2021, bleaching-susceptible *P. compressa* had 50% lower chlorophyll-*a* content than bleaching-resistant conspecifics (Fig. 4*F*). The individual effects of time (χ^2 = 24.67, $P < 0.0008$) and coral species (χ^2 = 46.8, $P < 0.0001$) also emerged as significant, where *P. compressa* had significantly greater chlorophyll-*a* content than *M. capitata* (up to 130%). Post hoc analyses revealed for both species chlorophyll-*a* content did not differ from the 2019 marine heatwave until 17 mo postheat stress (March 2021) ($P < 0.0001$), when chlorophyll-*a* was greatest, yet, in June 2021 and September 2022, chlorophyll-*a* declined to values indistinguishable from the heatwave ($P > 0.91$) (Fig. 4*F* and *SI Appendix,* Fig. S7). Metabolic rates, immunity [i.e., melanin content, prophenoloxidase (PPO)] and total antioxidant capacity (TAC) were influenced by the interaction of coral species and time, with all significant patterns detailed in Fig. 4 *G–L* and *SI Appendix,* Fig S7.

Multivariate Physiology Reveals Divergent Responses across Species and Time. For both *M. capitata* and *P. compressa*, permutational multivariate ANOVA (PERMANOVA) of physiological traits revealed a significant effect of time ($P < 0.0001$) (*SI Appendix,* Table S9). Pairwise comparisons revealed that multivariate physiology for all time points were significantly different from the marine heatwave for both species ($P < 0.005$) (Fig. 5). For *M. capitata*, all other comparisons were significantly different, apart from November 2020 and October 2021 ($P = 0.11$) and June 2021 and October 2021 ($P = 0.21$). For *P. compressa* after >1 y recovery from the marine heatwave, multivariate physiology indicated seasonal patterns, with no significant differences uncovered between August 2020 and September 2022 ($P = 0.26$), November 2020 and October 2021 ($P = 0.16$), and March 2021 and March 2022 ($P = 0.62$).

Standardized Acute Heat Stress Assays Confirm That Environmental Memory Influences Heat Tolerance. Photochemical yield (F_v/F_m) was significantly influenced by the interaction between treatment and species (X^2 = 35.3, $P < 0.0001$) as well as treatment and phenotype (X^2 = 9.1, $P = 0.03$) (*SI Appendix,* Table S10). For both species, significant declines in photochemical yield were only observed in the most extreme treatment ($P < 0.0001$), declining by over 50% in most individuals (Fig. 6). Further, regardless of species, significantly lower photochemical yield was found in bleaching-susceptible compared to bleaching-resistant corals at +9 °C ($P = 0.01$), whereas no detectable differences in phenotype were found between the three other treatments ($P > 0.74$). There was a 1.18 °C range in ED50 (effective dose 50) between the two species, with *P. compressa* more heat tolerant than *M. capitata*. Bleaching-susceptible *M. capitata* were the least heat tolerant, with a 50% reduction in F_v/F_m observed at 36.1 °C (95% CI: 35.8 to 36.5 °C) vs. 36.6 °C (95% CI: 36.3 to 36.9 °C) for bleaching-resistant conspecifics (Fig. 6*C*). For *P. compressa*, bleaching-susceptible corals were virtually indistinguishable from bleaching-resistant phenotypes, with a 50% reduction in F_v/F_m observed at 37.2 °C (95% CI: 36.7 to 37.6 °C) and 37.3 °C (95% CI: 36.8 to 37.8 °C), respectively. Color scores revealed similar patterns, with bleaching-susceptible *M. capitata* exhibiting lower ED50 (34.2 °C; 95% CI: 33.3 to 35.1 °C) than bleaching-resistant conspecifics (34.5 °C; 95% CI: 33.7 to 35.3 °C) (Fig. 6*D*). For *P. compressa*, color score
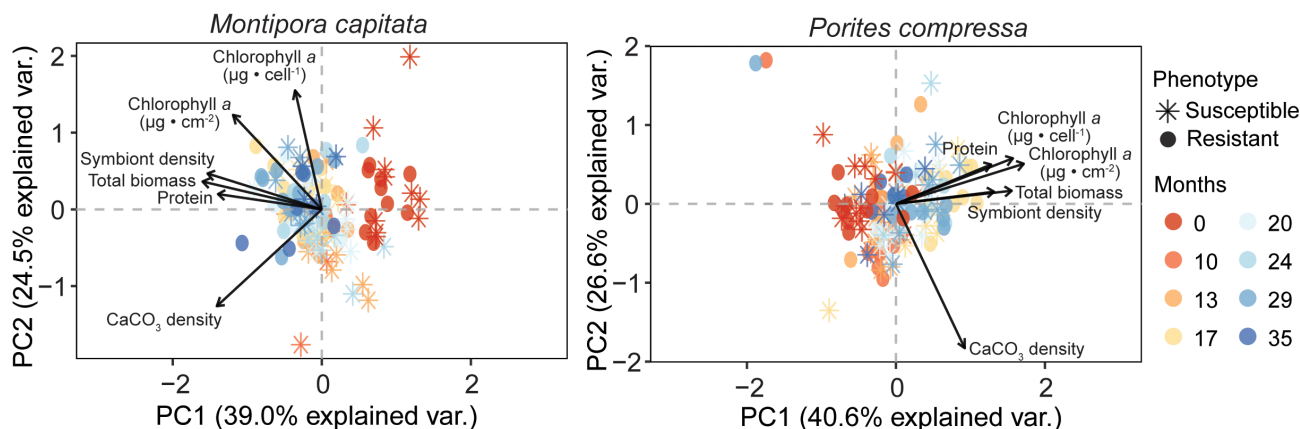
Fig. 5. Principal component analysis (PCA) of physiological traits of individual bleaching-resistant and bleaching-susceptible corals over time. Biplot vectors represent physiological traits (solid arrows), and points indicate the multivariate physiology of each coral genet (n = 4 to 10). Colors of the points indicate the number of months postheat stress, where "0" (red) represents the 2019 marine heatwave.

ED50 was indistinguishable between bleaching-resistant and bleaching-susceptible *P. compressa* phenotypes (34.4 °C and 34.6 °C, respectively) (Fig. 6D).

Discussion

Legacy Effects of Successive Heatwaves Have Led to Annual Bleaching in Susceptible *M. capitata*. Bleaching-susceptible colonies of *M. capitata* are now experiencing annual seasonal bleaching in the absence of anomalously high temperatures after a decade that included three marine heatwaves. This phenomenon

was initially observed in the first summer following the 2015 heatwave and was likely exacerbated by the combined impacts of the back-to-back heatwaves in 2014 and 2015 (36, 37). Encouragingly, in the second year after that heatwave, bleaching-susceptible *M. capitata* regained pigmentation over the winter and did not bleach again the following fall, indicating a ~2-y recovery period. Yet, when faced with a third marine heatwave just 4 y later (2019), these same *M. capitata* colonies bleached again even though the heatwave was less severe. Declining performance in response to a second heatwave has been observed in corals from Australia (29) to the Caribbean (28); however, that bleaching-susceptible
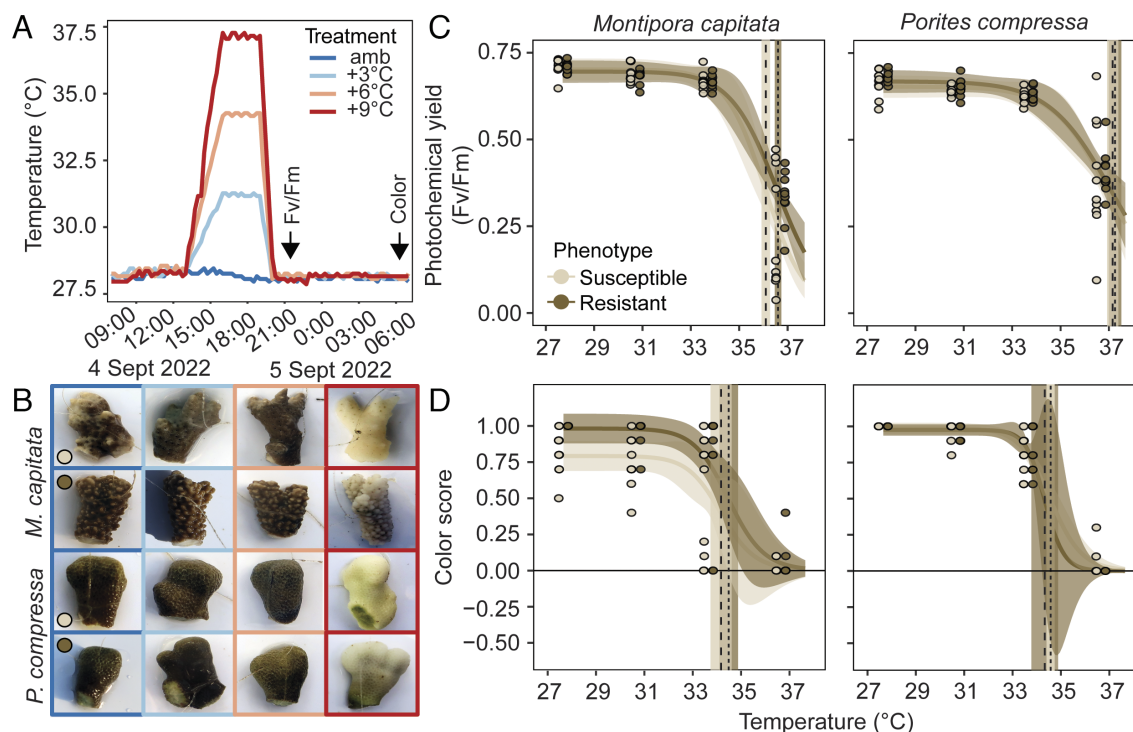
Fig. 6. Variation in heat tolerance across bleaching-susceptible and bleaching-resistant corals from experimental heat stress assay. (*A*) Temperature measurements (recorded every 15 min) of the controlled experimental heat stress assays (amb = ambient temperature of 27.7 °C), with an arrow indicating when dark-adapted photochemical yield (F_v/F_m) and color score were determined. (*B*) Respective images of coral fragments during the short-term heat stress. Three-parameter log-logistic dose–response curves were fitted to (*C*) F_v/F_m measurements (±95% CI) and (*D*) color score measurements (±95% CI) in response to temperature for *M. capitata* and *P. compressa*, where points indicate individual measures for coral genets (n = 10) in each treatment. Dashed vertical lines indicate the mean ED50 for each phenotype (dashed = susceptible, dotted = resistant), with the SE indicated by the shaded regions based on individual curve fits for each coral genet. The ED50s of photochemical yield for each coral/phenotype were 36.1 °C *M. capitata* (susceptible), 36.6 °C *M. capitata* (resistant), 37.2 °C *P. compressa* (susceptible), 37.3 °C *P. compressa* (resistant). The ED50s of the color scores for each coral/phenotype were 34.2 °C *M. capitata* (susceptible), 34.5 °C *M. capitata* (resistant), 34.6 °C *P. compressa* (susceptible), 34.4 °C *P. compressa* (resistant).

M. capitata colonies repeatedly bleached during each of the three summers following the 2019 event, in the absence of thermal stress, is alarming. While seasonal declines in coral biomass and symbiont density during summer temperatures are common (38, 39), they do not typically lead to the visually apparent bleaching observed here. These results indicate that the frequency of heatwaves in Hawai'i over the past decade has compounded the stress experienced by susceptible corals, leading to persistent declines in performance under ambient conditions. Furthermore, bleaching-susceptible individuals had higher partial mortality (~20%) than bleaching-resistant conspecifics (<5%) following the 2015 heatwave (33), underscoring the ecological significance of these differential responses. Encouragingly, bleaching-resistant individuals within this same population of *M. capitata* have remained consistently pigmented across multiple heatwaves and were 0.5 °C more heat tolerant than bleaching-susceptible conspecifics 3 y after the 2019 event. However, higher bleaching thresholds surprisingly did not translate into greater survival in the 3 y following the 2019 heatwave, indicating that the accumulation of stress following three successive heatwaves in under a decade negated the survival benefits of bleaching-resistance.

Physiological data further confirmed that resistance to bleaching in *M. capitata* was not a sufficient measure of coral performance. Specifically, we observed incomplete recovery across multiple phenotypic and physiological metrics in both bleaching-resistant and bleaching-susceptible individuals in the 3 y following the 2019 marine heatwave, highlighting a legacy of stress that transcended visual bleaching assessments and persisted for several years. For example, neither phenotype exhibited complete recovery in symbiont or host protein densities during the 3-y period following the 2019 heatwave. At their peak (after 35 mo of recovery), symbiont densities only reached up to half of preheatwave densities [January 2014: 4 to 5×10^6 cells cm^{-2} (40)]. Given the ongoing upward trajectory, symbiont recovery will likely continue so long as another heatwave does not occur. These results underscore that physiological recovery can be a multiyear process, even when visual recovery is apparent within a few weeks to months following heat stress (37, 41). Interestingly, not all physiological parameters demonstrated a lag in recovery, with tissue biomass and lipid densities displaying apparent recovery followed by strong seasonality in the first year post heat stress. However, traits important for coral fitness, such as growth and fecundity, can take 4 y or more to recover following heat stress (18, 42–44). Long-term investigations are clearly needed to observe recovery in metrics closely linked to fitness as marine heatwaves continue to increase in frequency and severity, and thus increasingly overlap with the time required by many corals to fully recover. Decreasing duration of periods of relief from thermal stress can compound physiological stress in many surviving corals, which may alter their relative performance and survival within communities (30) and will have important ramifications for community composition and ecosystem function.

A better understanding of the mechanisms driving bleaching resistance may help predict the fate of corals in future reefs. For example, thermal tolerance in *M. capitata* is associated with a combination of host (31) and symbiont (45) factors. In Kāne'ohe Bay, *M. capitata* can host *Cladocopium* (ITS2-type "C31") and *Durusdinium glynnii* (46–48), and bleaching resistance is strongly correlated with higher proportions of *D. glynnii* (45). Indeed, the bleaching-susceptible colonies observed here hosted almost exclusively *Cladocopium* spp., while bleaching-resistant colonies predominantly hosted *D. glynnii* (31, 49) (*SI Appendix*, Table S11). Both phenotypes exhibited additional physiological signatures of *Cladocopium*- or *Durusdinium*-dominated symbioses, respectively. For example, bleaching-susceptible *M. capitata* had nearly half as many symbionts as bleaching-resistant colonies across all seasons, matching observations that *Cladocopium*-dominated *M. capitata* tend to have lower symbiont densities than *Durusdinium*-dominated colonies (34, 37). While *Durusdinium*-dominated *M. capitata* were able to maintain bleaching resistance and higher symbiont densities, *D. glynnii* generally provides the host with fewer resources than *Cladocopium* spp. under both ambient and heat stress conditions (50), indicating that symbiont retention during heat stress is an incomplete measure of coral performance. However, the nutritional benefits of hosting *Cladocopium* spp. may diminish over time as heatwaves and bleaching become increasingly common, and the impacts of changing symbiont dominance on coral growth and survival, and thus ecosystem function, require further study.

Environmental Memory of Heatwaves Has Led to Beneficial Acclimatization in *P. compressa*. Bleaching-susceptible and bleaching-resistant *P. compressa* appear to have converged on the same resistant phenotype despite past differences in bleaching susceptibility. Surprisingly, neither phenotype bleached significantly during the 2019 heatwave, even though the bleaching-susceptible colonies exhibited severe bleaching and some (~20%) partial mortality during the 2015 heatwave (33, 34). While lower bleaching severity in 2019 may have been due to somewhat lower levels of heat stress accumulation than in 2015, experimental heat stress tests confirmed identical bleaching thresholds in bleaching-susceptible and bleaching-resistant phenotypes, and neither phenotype experienced significant mortality following the 2019 event. Together, these results indicate that beneficial acclimatization occurred and has persisted for several years in this species. Higher bleaching thresholds have been observed in multiple coral species following successive marine heatwaves (17–21), supporting the hypothesis that environmental memory of a prior stress event improves the response to a subsequent exposure, and is a common capability in corals. Increases in bleaching resistance from 2015 to 2019 were also observed in *P. compressa* across the population, which may also have stemmed from beneficial acclimatization; however, selection against weak corals or symbioses (20, 23, 30) or a shift to more stress-tolerant symbionts (30) is also possible. Support for these latter two hypotheses is limited for *P. compressa* in Kāne'ohe Bay, where i) whole-colony mortality was low in the aftermath of the 2014 and 2015 heatwaves (33, 36), ii) *P. compressa* does not exhibit evidence of cryptic host speciation (51), and iii) *P. compressa* maintains a specific symbiosis with a single symbiont species, *Cladocopium* ITS2-type "C15" (46). By following individual colonies across multiple heatwaves, this study indicates that the heatwaves in 2014 and 2015 resulted in stress hardening, not loss of sensitive individuals from the population, that first manifested as a decrease in bleaching severity in 2019, and this benefit has persisted within individuals for nearly a decade. While the exact mechanisms conferring this resilience have not been determined, physiological plasticity (18, 37), constitutive upregulation of stress-response genes (52, 53), and epigenetic modifications (54) all likely contribute and represent important avenues of future study. Importantly, whether the benefits of environmental memory of moderate heat stress will persist as heatwaves become more intense remains unknown.

In the years following the 2019 heatwave, both phenotypes of *P. compressa* exhibited physiological recovery across multiple traits, requiring ~1.5 y to reach symbiont, chlorophyll-*a* and protein densities similar to historical preheatwave levels (55). Given their faster recovery and elevated bleaching thresholds (+0.7 to 1.2 °C) relative to *M. capitata*, *P. compressa* may become more dominant in this region as heatwaves become more frequent. Indeed, *M. capitata*

exhibited greater partial mortality (Fig. 2) and greater declines in benthic cover than *P. compressa* following the 2019 event (56), although both species experienced significant mortality across Kāneʻohe Bay in 2019 [19% decline in *P. compressa*, 23% decline in *M. capitata* (56)]. Greater bleaching resistance and lower mortality favors the dominance of *P. compressa,* which already reaches >75% cover on some reefs in Kāneʻohe Bay (57). While high coral cover persists in this location despite bleaching-related mortality of these two dominant species, and has historically been considered a key metric of reef condition, the loss of biodiversity associated with transitioning from a multispecies assemblage to a predominantly *P. compressa* landscape would likely have a multitude of adverse effects on ecosystem function, from declining coral productivity to losses of blue food security (10, 58). Further, critical processes such as reef accretion are projected to become uncoupled from coral cover under global change (59). Here, *P. compressa* was unable to sustain skeletal density as high as *M. capitata*, despite maintaining up to three times higher coral cover and exhibiting less bleaching and mortality. These patterns may be explained by: i) enhanced heat tolerance resulting in trade-offs with growth [(60, 61 but see ref. 62), and/or ii) the duration of our study was not long enough to capture the recovery of secondary calcification (i.e., densification) for this species, as recurring marine heatwaves could have delayed the revival of densification. Indeed, *P. compressa* are unable to recover calcification rates in the first 8 mo following heat stress (63), and elsewhere in the Pacific, *Porites* spp. can exhibit growth hiatuses for up to 4 y in the aftermath of a marine heatwave (44). Whether modern reefs are able to maintain net accretion and continue to provide the critical ecosystem services humans rely on remains to be seen.

Conclusions. We have entered a new era of ocean warming that is affecting coral reefs in ways we are only just beginning to understand. Corals in the Main Hawaiian Islands have experienced a rise in offshore sea-surface temperatures of 1.15 °C in the last 60 y (64, 65), leading to an unprecedented three coral bleaching events in the last decade (2014 to 2023) that were preceded by a single widespread coral bleaching event (1996) the entire century prior (57, 66). The responses of individual corals to these increasingly frequent heatwaves demonstrate the divergent intra- and interspecific bleaching and recovery trajectories possible within a single coral community, highlighting the challenge of predicting future coral performance in a changing ocean. In one direction, *P. compressa* that were highly sensitive to marine heatwaves in 2014 and 2015 (i.e., severely bleached) have become visually and physiologically indistinguishable from bleaching-resistant conspecifics during a third heatwave (2019) and during extreme heat stress tests, indicating beneficial acclimatization that persists across many years. This increase in bleaching resistance was accompanied by rapid physiological recovery after repeat heat stress, although there remained evidence of persistent stress (e.g., weakened skeletons), suggesting that these corals may undergo tradeoffs that can erode ecosystem function. Increases in coral bleaching resistance across recurring heatwaves have become more prevalent on reefs across the globe (15, 17, 19, 21), which is encouraging, as avoiding bleaching is often associated with greater survival (33) and stress hardening may thus promote the persistence of corals in our warming oceans. On the other hand, the extent of coral mortality has been increasing with each successive heatwave in this system, from <1% in 1996 to 13% in 2014, 22% in 2015, and >20% in 2019 (56, 67). Furthermore, bleaching-susceptible *M. capitata* are visibly struggling from the recent barrage of heatwaves, manifesting as annual seasonal bleaching and escalating partial mortality in the absence of measurable heat stress. Importantly, even bleaching resistance was not associated with greater

survival or recovery capacity in *M. capitata*, highlighting the danger of predicting future individual performance and reef function from a lack of visual bleaching alone. The inability of *M. capitata* of either bleaching phenotype to recover physiologically after 3 y following a repeat heatwave underscores that coral resilience is a multifaceted trait beyond bleaching resistance (60) and brings into question how we define coral resilience in the context of global change. Now, more than ever, seasonal and long-term studies are critically needed to identify corals that cannot just withstand and survive repeated heat stress events, but also rapidly recover ecosystem-defining traits (e.g., biomineralization) to continue providing the critical ecosystem services coastal communities directly rely on. Urgent, collective global action to eliminate greenhouse gas emissions remains the only approach that may provide sufficient time for corals to acclimatize and adapt to rapid climate-induced temperature increases in order for coral reef ecosystems to persist in the Anthropocene.

Materials and Methods

Study Site and Seawater Temperature. This study was conducted at PR13 in the southern region of Kāneʻohe Bay, Oʻahu, Hawaiʻi. Seawater temperatures were recorded from January 2014 to April 2023. Where the record was incomplete, temperature data from two nearby reefs (<0.5 km away) were included. Cumulative heat stress (DHW) was determined following the equations in ref. 68 using the maximum monthly mean (MMM) of 27.3 °C. These results were compared to DHW on the reef of Moku o Loʻe (PR1), and vs. DHW using the regional MMM of 27.0 °C and MMM used in the literature for Kāneʻohe Bay [27.7 °C (37); 28.0 °C (34, 69)] (*SI Appendix*).

Coral Bleaching and Mortality Assessments. Adjacent conspecific corals with contrasting bleaching phenotypes (i.e., bleaching-resistant vs. bleaching-susceptible) were first identified during the 2015 marine heatwave (33). A total of 10 colonies per phenotype per species of *M. capitata* and *P. compressa* were followed for this study. Colonies of *M. capitata* were previously confirmed to be distinct genotypes (31), and *P. compressa* has very low clonality in this area (70). Bleaching severity and partial mortality of each colony was determined from photographs taken between October 2015 to April 2023 (*SI Appendix*). Coral cover and reef-wide bleaching prevalence were also determined at each time point from benthic photoquadrats as in refs. 33 and 34 (*SI Appendix*).

Physiological Analyses. Fragments from each colony were collected across eight time points from October 2019 to September 2022. Photosynthetic rates were assessed at increasing irradiance via changes in oxygen evolution as previously described (34) (*SI Appendix*, Fig. S8). Coral fragments were then flash-frozen in liquid nitrogen and stored at −80 °C until further processing. Coral tissue was removed from skeletons with a waterpik, and host and symbiont fractions were separated by differential centrifugation. All details of host (tissue biomass, protein and lipid concentrations, TAC, melanin content, PPO activity, and $CaCO_3$ density) and symbiont (symbiont density and chlorophyll-*a* concentration) analyses can be found in *SI Appendix*.

Acute Heat Stress Experiment. Ten individual colonies of each phenotype per species were sampled at the end of summer (September 1, 2022) and assessed for heat tolerance following a standardized protocol (35, 71). Briefly, corals were exposed to a 3-h ramp to respective treatment temperatures (ambient: 28.0 °C; amb+3 °C: 31.0 °C, amb+6 °C: 34.0 °C, and amb+9 °C: 37.0 °C), a 3-h hold, and a 1-h ramp down to ambient. At the end of the ramp and 1 h after sunset (~19:30), corals were assessed for photochemical yield (F_v/F_m). The following morning corals were photographed with a color standard to assess coral color (Fig. 6 and *SI Appendix*).

Statistical Analyses. All statistical analyses were done using R version 4.0.3 software (72) and are explained in detail in *SI Appendix*, Table S12. Briefly, a linear model was used to test for differences in colony-level bleaching severity between species, phenotype, season, and time. Linear mixed effects models were used to assess for differences in physiological parameters. Differences in coral multivariate phenotypes were analyzed separately for each coral species using PERMANOVA and principal component analysis, with the fixed effects phenotype and months post heat stress. To determine how heat tolerance differed among

coral species and phenotype, dose–response curves were fit to the median F_v/F_m across temperature treatments, and the effective temperature to induce a 50% loss in F_v/F_m (ED50) was calculated as the F_v/F_m or color score from the model fit that is 50% of the initial value (71).

Author affiliations: [a]Department of Biology, University of Pennsylvania, Philadelphia, PA 19104; [b]University of Hawai'i Sea Grant College Program, University of Hawai'i at Mānoa, Honolulu, HI 96822; [c]Daniel K. Inouye Center for Microbial Oceanography: Research and Education, Department of Oceanography, University of Hawai'i at Mānoa, Honolulu, HI 96822; [d]Hawai'i Institute of Marine Biology, University of Hawai'i at Mānoa, Kāne'ohe, HI 96744; and [e]Department of Biological Sciences, University of Rhode Island, Kingston, RI 02881

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