Coral bleaching response is unaltered following acclimatization to reefs with distinct environmental conditions

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Urgent action is needed to prevent the demise of coral reefs as the climate crisis leads to an increasingly warmer and more acidic ocean. Propagating climate change–resistant corals to restore degraded reefs is one promising strategy; however, empirical evidence is needed to determine whether stress resistance is affected by transplantation beyond a coral’s native reef. Here, we assessed the performance of bleaching-resistant individuals of two coral species following reciprocal transplantation between reefs with distinct pH, salinity, dissolved oxygen, sedimentation, and flow dynamics to determine whether heat stress response is altered following coral exposure to novel physicochemical conditions in situ. Critically, transplantation had no influence on coral heat stress responses, indicating that this trait was relatively fixed. In contrast, growth was highly plastic, and native performance was not predictive of performance in the novel environment. Coral metabolic rates and overall fitness were higher at the reef with higher flow, salinity, sedimentation, and diel fluctuations of pH and dissolved oxygen, and did not differ between native and cross-transplanted corals, indicating acclimatization via plasticity within just 3 mo. Conversely, cross-transplants at the second reef had higher fitness than native corals, thus increasing the fitness potential of the recipient population. This experiment was conducted during a nonbleaching year, so the potential benefits to recipient population fitness are likely enhanced during bleaching years. In summary, this study demonstrates that outplanting bleaching-resistant corals is a promising tool for elevating the resistance of coral populations to ocean warming.

Significance

Ocean warming has caused catastrophic losses of corals on reefs worldwide and is intensifying faster than the adaptive rate of most coral populations that remain. Human interventions, such as propagation of heat-resistant corals, may help maintain reef function and delay further devastation of these valuable ecosystems as society confronts the climate crisis. However, exposing adult corals to a complex suite of new environmental conditions could lead to tradeoffs that alter their heat stress responses, and empirical data are needed to test the utility of this approach. Here, we show that corals transplanted to novel reef conditions did not exhibit changes in their heat stress response or negative fitness tradeoffs, supporting the inclusion of this approach in our management arsenal.

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Determining the feasibility of these approaches therefore requires improved knowledge of the fundamental mechanisms of coral acclimatization, since we do not know whether or for how long these phenotypes are retained following exposure to novel environmental regimes within or across generations. Rigorous experimental evaluation that incorporates the complexity of the natural reef environment is therefore needed to address this question, the results of which are important not only for restoration but also for understanding the capacity for coral populations to withstand rapid environmental change resulting from anthropogenic activities.

A first step in testing whether bleaching resistance is the result of local adaptation or acclimatization is to identify individuals with higher temperature thresholds for bleaching within a population. Bleaching-resistant corals are often found in locations with higher mean temperatures [e.g., shallow inshore reefs with restricted water flow (30–32)] or those with larger magnitude or higher frequency fluctuations in temperature than surrounding reefs (33–36), though not always (37). Reefs with conditions that promote these local threshold maxima are likely excellent resources for selecting the most bleaching-resistant genets of the various species found in a region but only if elevated heat tolerance is retained when environmental conditions change. There is evidence of local adaptation to different thermal regimes between populations (38–41) and that heat tolerance can be heritable (42–45), yet much remains to be learned about mechanisms determining bleaching tolerance within populations. In particular, acclimatization can contribute to gains in heat tolerance (34), yet adult corals can also maintain their relative (if not absolute) bleaching performance following acclimatization in common garden settings (41, 46). It is therefore critical to understand the relationship between acclimatization and genotype-specific fixed effects in determining coral bleaching thresholds, as both these mechanisms influence the persistence of adaptive traits through time and space (47).

Coral bleaching events provide an opportunity to identify bleaching-resistant individuals within populations already exhibiting higher mean bleaching thresholds and have the advantage of allowing assessment of relative performance in a natural context. Here, we identified bleaching-resistant individuals of two important reef-building species, Montipora capitata and Porites compressa, from a site with higher bleaching thresholds relative to nearby reefs (48). Bleaching-resistant coral genets were identified here as those that remained fully pigmented while as much as 79% of live coral bleached during the peak of a coral bleaching event that occurred in a Kane‘ohe Bay, Hawai‘i in 2015 (49), the second of two consecutive annual bleaching events in the region (50). After allowing for one year of recovery from the heat stress event, the effects of acclimatization to a novel physicochemical environment on coral acute heat stress response and fitness were tested by reciprocally transplanting ramets of each genet between two patch reefs with distinct environmental conditions. In addition, the physiological plasticity of each species was examined by measuring coral survival, growth, metabolism, tissue energetics, and feeding rates in their native versus cross-transplanted environments at 3 and 6 mo posttransplantation. These experiments are a critical step toward understanding the biological basis and utility of selecting and propagating climate change–resistant corals for enhancing coral reef resilience to climate change.

Results
Distinct Physicochemical Dynamics Characterized Each Reef. Temperature and light dynamics were similar between the two patch reefs (Fig. 1A and B and SI Appendix, Table S1 and Figs. S1 and S2), as were mean pH, dissolved oxygen (DO), and light (SI Appendix, Table S1). In contrast, salinity differed between the two sites (Fig. 1C and SI Appendix, Fig. S1), and diel fluctuations in pH and DO were 2.92-fold and 2.68-fold greater at the Outer Lagoon than the Inner Lagoon reef, respectively (Fig. 1D and E and SI Appendix, Fig. S1 and Table S1). Sedimentation rates were 8.27-fold higher at the Outer Lagoon (0.324 ± 0.066 g·day⁻¹) than the Inner Lagoon reef (0.039 ± 0.003 g·day⁻¹; SI Appendix, Table S1), and relative flow rates were approximately twofold higher at the Outer Lagoon reef (SI Appendix, Table S1).

Coral Fitness Differed between Reefs but No Evidence of Site Specialization or Tradeoffs. Improvements in performance of M. capitata cross-transplanted to the Outer Lagoon reef did not incur a tradeoff with reproduction, as there was no relationship between growth and fecundity (SI Appendix, Fig. S9). In the reverse direction, cross-transplants of M. capitata at the Inner Lagoon reef that had a decline in overall performance showed a strong positive relationship between growth and reproduction (P < 0.005, r² = 0.700; SI Appendix, Fig. S9), whereas native corals at both reefs showed no relationship between growth and reproduction, indicating that there were no negative tradeoffs between growth and reproduction for any of the four transplant histories. Because the fitness of coral transplants depends on their ability to survive and reproduce in their new environment and because reproductive output of colonial organisms like corals is positively correlated with size (51), an integrative metric of coral fitness was calculated as the product of survival, growth, and (for M. capitata only) reproductive success of each genet. Corals at the Outer Lagoon reef showed significantly higher fitness scores than corals at the Inner Lagoon reef, but there were no differences in fitness between native and cross-transplanted corals at the Outer Lagoon reef (Fig. 3A and B and SI Appendix, Tables S20 and S21). In contrast, at the Inner Lagoon reef, cross-transplants of M. capitata displayed higher fitness than native corals but only when accounting for differences in reproductive success (Fig. 3A and SI Appendix, Tables S20 and S21). Local specialization of each genet was calculated by considering its relative fitness in its native versus cross-transplanted environment. In general, corals exhibited positive specialization values at the Outer Lagoon reef, whereas corals native to the Inner Lagoon reef showed negative specialization values (Fig. 3C and D), indicating corals performed better at the Outer Lagoon reef even when it was not their native environment. One genet of P. compressa native to the Inner Lagoon had a positive local specialization score

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and was the only genet of either species native to the Inner Lagoon that had higher fitness at its native reef (Fig. 3D).

Coral Acute Heat Stress Response Was Unaffected by Transplantation. At the initiation of the acute heat stress aquarium experiment (maximum daily temperature of 27 °C across all treatments; SI Appendix, Fig. S10), there were no significant differences in performance metrics (i.e., light-enhanced dark respiration [LEDR], Fv/Fm, and gross photosynthesis) between species, treatments, origins, or destinations (SI Appendix, Fig. S11). At the end of the 10-d heat stress, the heat treatment reached a daily maximum of 32 °C (maximum monthly mean 4 °C), while the ambient treatment reached a daily maximum of 28 °C (SI Appendix, Fig. S10). Linear mixed models (SI Appendix, Table S22) indicated that temperature was a significant factor across all parameters examined, with corals in the heat treatment exhibiting declines in photochemical yield (Fig. 4A and SI Appendix, Table S23), metabolic rates (Fig. 4B and C and SI Appendix, Table S24), and calcification rates (Fig. 4D and SI Appendix, Table S25). Origin was not a significant factor for any of the metrics examined (Fig. 4 and SI Appendix, Tables S23–S25), indicating that there was no decline in the heat stress response capacity of cross-transplanted corals relative to ramets that remained at their native reef, and thus, exposure to a novel environment did not alter heat stress responses of these bleaching-resistant corals. Overall, *P. compressa* showed the greatest declines in performance metrics in response to heat stress, with declines in photochemical yield, photosynthesis, and calcification exceeding those of *M. capitata* (Fig. 4 and SI Appendix, Tables S23–S25).

Discussion

Coral Heat Stress Responses Unaffected by Transplantation. Transplantation of bleaching-resistant corals to a novel environment in situ did not alter their heat stress response, despite transplants exhibiting high levels of phenotypic plasticity for other traits. Because bleaching-resistant corals tend to have lower mortality (49) and higher reproductive success (7, 52, 53) than bleaching-sensitive conspecifics following a bleaching event, they have a clear selective advantage during and in the years following these events. Harnessing these natural advantages by propagating bleaching-resistant individuals is a promising approach to maintain reef function increasing the bleaching resistance of a population using native (i.e., endemic, local) coral stocks. Furthermore, relative bleaching resistance of *M. capitata* and *P. compressa* has persisted through multiple in situ bleaching events (54, 55), indicating that bleaching resistance is retained and will likely continue during future heatwaves.
of similar magnitude. This, in combination with heat stress response being unaffected by both transplantation and acclimatization to a complex in situ environment, makes bleaching resistance a promising trait for selecting individuals to enhance resistance of coral populations to climate change. Finally, because *M. capitata* and *P. compressa* represent divergent lineages of two globally distributed coral genera, these patterns may be shared with species on reefs around the world.

**Fitness Consequences of Coral Acclimatization to Novel Environments.** The identification of negative tradeoffs during acclimatization is important for informing trait-guided restoration. Indeed, corals acclimatizing to new thermal regimes can exhibit declines in growth and/or reproduction (38, 40), reducing the potential benefits of their introduction. Here, despite corals exhibiting high levels of phenotypic plasticity across a range of traits including metabolism, feeding, growth, and reproduction following transplantation to reefs with distinct physicochemical conditions, negative tradeoffs were not observed for either species. In general, corals at the Outer Lagoon performed better overall, and improvements in any one trait did not come at the cost of another. These results are consistent with data from other reef systems that demonstrate an absence of tradeoffs between bleaching and reproduction (56) and between resistance traits against multiple stressors (57) and holds promise that these bleaching-resistant genets may also withstand additional stressors. Critically, bleaching-resistant cross-transplants maintained fitness equal to or higher than that of native corals, despite having acclimatized to substantially different environmental regimes. This indicates that these corals would have a neutral or positive effect on the fitness of recipient populations, even during a nonbleaching year, and would likely elevate the recipient population’s fitness during future heatwaves due to their greater bleaching resistance. The duration of elevated fitness in cross-transplants, which lasted at least 11 mo in this study, remains unknown and could be the result of a temporary carryover of the energetic benefits of having originated from a more favorable reef environment. This potential lag effect, as well as seasonal cycles, have been shown to affect corals on an annual cycle (e.g., refs. 58 and 59), and future work is needed to assess multiyear influences on coral fitness. However, even if this carryover were transient, the long-term fitness effects for recipient populations are likely net positive due to the transplants’ higher expected relative performance during increasingly common marine heatwaves. These results are a necessary first step to validate trait-guided approaches in...
reef restoration and adaptive management. Additional work is needed to determine the persistence of these traits in the population, which requires they be both heritable, as has been shown for several species (42–45), and introduced in sufficient abundance. Initial studies indicate that stress-resistant corals must be introduced in numbers equivalent to at least 2 to 5% of the population per year for several decades in order to achieve adaptive gains in heat tolerance that can keep pace with climate change (60). As such, work is needed to scale up these approaches if they are to have a meaningful impact on coral reef resistance to ocean warming. However, this approach cannot work in isolation, and it is imperative that investments in adaptive management are supported by strong local measures to maintain water quality and limit overfishing (61, 62). In addition, these measures cannot

![Fitness score for (A) M. capitata and (B) P. compressa. Fitness score is a product of net growth and survival (G*S; solid lines) and for M. capitata was also calculated as the product of net growth, survival, and reproductive success (G*S*R; dashed lines). n = 10; error bars indicate SEM. Magnitude of local specialization for each genet of (C) M. capitata and (D) P. compressa. Local specialization values are defined as the difference in fitness score (G*S only) of a genet at its origin and destination reef, divided by the mean fitness score of all conspecifics at the destination reef. Positive values indicate local site specialization; negative values indicate destination reef favorable.](image1)

**Fig. 3.**

![Coral performance following acute heat stress (high temperature; 32 °C) versus controls (ambient temperature; 27 to 28 °C). (A) Photosynthetic efficiency (dark-adapted yield; Fv/Fm), (B) gross photosynthesis rates, (C) LEDR rates, and (D) calcification rates. n = 8 to 10; error bars indicate SEM. Inset indicates statistically significant fixed effects (S, species; T, temperature; D, destination).](image2)

**Fig. 4.**

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mounting evidence that the current rate of ocean warming is not always be

**Genotype–Environment Effects.** Despite consistently higher mean coral performance at the Outer Lagoon reef, in many cases, these differences in performance between the two reefs for an individual trait may not be significant due to a strong genotype-environment (GxE) effect. Growth in particular showed a strong GxE effect, aligning with recent work cautioning against using growth alone as a predictive trait for future coral performance as it can vary across time (63, 64). Furthermore, heat tolerance in a stressful environment does not ensure rapid growth in a less stressful environment (65). Our results do support the need for a genetically diverse “planting stock” to account for the wide range of expressed phenotypes in different reef environments (66). In summary, this study indicates that heat stress response was not plastic in *M. capitata* and *P. compressa*, and past bleaching resistance is thus likely indicative of future coral performance.

**Biologically Guided Strategies for Coral Reef Restoration.** There is mounting evidence that the current rate of ocean warming is outpacing the “natural” dispersal rate of heat-tolerant genets and the generation times required for adaptation to increase heat tolerance of coral populations (67). This reality underscores the need for scientifically informed human interventions in management and restoration. Here, we show that the heat stress response of bleaching-resistant corals was unaltered following transplantation into novel environments, and this was accomplished without incurring fitness costs. While more work is needed to determine how well bleaching resistance persists across generations, these results support the use of active restoration for promoting climate resilient reefs. Additional traits are also important when selecting individuals for restoration [e.g., ocean acidification tolerance, disease resistance, and genetic diversity (68)], although the plasticity of many of these traits are not well described. Encouragingly, relative growth during acidification stress is consistent in several coral species (69) and thus, along with bleaching resistance, may be a useful selection marker for promoting climate change resilient reefs via active management.

Site selection for nurseries and outplanting is also an important consideration to maximize restoration success, as water quality is critical for outplant survival (62) and can be managed at the local level. Here, we found that the reef with the greatest water flow, *diel* physicochemical variation, and distance from land resulted in higher coral growth and fitness. Sufficient water flow is generally beneficial for coral performance across reef systems (70), and both flow and temperature variability can mitigate bleaching responses (21, 36, 70), indicating that these may be generalizable environmental characteristics of reefs that promote coral fitness and bleaching resistance (although, for exception, see ref. 37). Our results highlight the importance of local management of water quality and ecosystem health (e.g., limiting fishing pressure) and the need to select sites for nurseries and outplanting that promote high coral fitness, as this could accelerate the successful establishment of corals. Furthermore, in situ nursery sites that promote faster growth would provide obvious logistical benefits, leading to shorter residence times for individuals and greater yields for outplanting. Assisted gene flow using climate change–resistant genets could complement traditional conservation measures such as marine protected areas, which could provide favorable habitat for stress-resistant outplants, and in coordination with less directed approaches [e.g., adaptation networks (71)] to preserve species diversity and promote reef resilience to climate change, temporarily buying these invaluable ecosystems time as society struggles with reigning in the current climate catastrophe.

**Materials and Methods**

**Site Selection and Characterization.** The coral-dominated patch reefs in the Kane‘ohe Bay lagoon (Fig. 1A) are exposed to distinct seawater conditions that result from spatial gradients within the lagoon driven by differences in seawater residence times (74), freshwater and nutrient input (75), and human influence (76). Here, we characterized the physicochemical conditions of two patch reefs with contrasting seawater residence times and terrestrial influence: 1) a nearshore Inner Lagoon reef (21.4343°N, 157.7991°W) with long seawater residence times (30° days) located 0.75 km from shore and 2) an offshore Outer Lagoon reef (21.4516°N, 157.7966°W) with short seawater residence times (<1 d) located 1.6 km from shore (Fig. 1A). Seawater temperatures, salinity, pH, and dissolved photosynthetically active adenine riboside (DPAR) were measured every 15 min above the reef benthos at each site (2 m depth). Sedimentation rates were measured every 2 wk, and relative water flow was measured at least monthly at each reef using the clad card dissolution technique (77).

**Reciprocal Transplant Setup.** During the peak of the 2015 coral bleaching event in Kane‘ohe Bay, bleaching prevalence for each of the two dominant reef-building corals, *M. capitata* and *P. compressa*, was up to 68 to 87% of the population, respectively (SI Appendix, Fig. S12). At that time, 10 bleaching-resistant (i.e., fully pigmented) colonies of each species were visually identified and tagged at both the Inner and Outer Lagoon reefs, and their health was monitored for the following year (SI Appendix, Fig. S12; (49)). One year later, a portion of each colony was collected from the reef and fragmented into ramets, and a reciprocal transplant was initiated where half of the ramets from each colony remained at their origin reef while the other half were cross-transplanted to the other reef.

**Coral Performance.** A total of 30 following translocation, coral survival was quantified for all fragments, and skeletal accretion, linear extension, and dark-adapted photochemical efficiency (Fv/Fm) were quantified for 10 fragments per parent per transplant treatment (n = 800). Half of these were transplanted to the field, and the other half were assayed for photosynthetic and LEDR rates, tissue biomass and lipid content, and skeletal surface area. A subset of these (one per parent per history; n = 80) were used to quantify heterotrophic feeding rates. All of the above measures were repeated for
Acute Heat Stress Challenge. A subset of coral fragments (two per genet per transplant site; 160 fragments total) were used for an acute heat stress experiment following 6 mo of acclimatization. The high-temperature treatment was ramped 1 °C per day for 6 d, reaching a maximum of 32.0 °C (maximum monthly mean [MMM] + 4 °C) for 5 d (treatment was ramped 1 °C per day for 6 d, reaching a maximum of 32.0 °C; for details, see SI Appendix, Fig. S10). Maximum temperatures in the ambient treatment ranged from 26 to 28.6 °C over the course of the experiment. Coral skeletal accretion, photochemical efficiency (Fv/Fm), photosynthesis, and respiration rates for each fragment were determined at the beginning and end of the experiment as described above.

**Statistical Analyses.** Statistical analyses were conducted in R Statistical Programming (80). Principal component analysis (PCA) was used to determine the percent variance explained by seven physiological variables (biomass, calcification, linear extension, gross photosynthetic rate, LDR, P.R, and survival) in the separation of the transplant groups. PCA was conducted on the scaled and centered data using the procram function in the Vegan package (81). Phenotypic plasticity of each genet was calculated as the PCA distance between that genet’s native versus cross-transplanted phenotype in two-dimensional trait space (i.e., PC1 versus PC2), which accounts for correlations among traits (as in ref. 82). Differences in plasticity were tested using a two-way ANOVA. Univariate analyses were performed using linear mixed-effect models and are described in detail in SI Appendix, Supplementary Methods and Table S1.

**Data Availability.** All raw data and scripts have been deposited in Zenodo and are publicly available (DOI: 10.5281/zenodo.4315627).

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**Corollary Section:**

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