

Environmental history shapes thermal tolerance in Hawaiian corals, with species-specific responses in *Montipora capitata* and *Porites compressa*

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Abstract

Understanding variation in coral thermal tolerance is critical for predicting coral responses and reef persistence under future ocean conditions. This study investigated thermal performance of two dominant Hawaiian reef-builders, *Montipora capitata* and *Porites compressa*, collected from three sites in Kāneʻohe Bay and one site in nearby Kailua Bay (Ulupaʻu). Corals were subjected to a controlled heat-stress assay, and photosynthetic efficiency was measured using Pulse Amplitude Modulation (PAM) fluorometry. Thermal tolerance was quantified as effective dose 30 (ED30), the experimental degree heating week (eDHW) exposure at which corals lost 30% of photosynthetic efficiency. Both species exhibited high thermal tolerance, with ED30 values ranging from 5.93 to 7.21 eDHW and mean values of 6.44 eDHW for *M. capitata* and 6.70 eDHW for *P. compressa*. Within Kāneʻohe Bay, thermal performance was similar for both species. In contrast, *P. compressa* from Ulupaʻu displayed significantly greater tolerance than Kāneʻohe conspecifics and all *M. capitata* populations. Together, these findings demonstrate that coral thermal tolerance is shaped by environmental history in a species-specific manner. This highlights the importance of selecting both appropriate species and source populations when identifying thermally resilience corals for restoration and conservation strategies in Hawaiʻi.

Introduction

The ability to adapt or acclimatize to continued warming ocean temperatures is critical for corals as sessile organisms. Many reef-building corals live near their upper thermal limits, and even acute thermal anomalies (1–2°C above mean monthly maxima) can trigger the loss of algal symbionts via bleaching^{1,2}. Coral bleaching results in reduced and sometimes even complete loss of photosynthetic efficiency, compromised coral health, and widespread mortality should stressful conditions persist^{3,4}. Bleaching thresholds vary among species, populations, and individual colonies, making it complex to understand the drivers of thermal tolerance and predict coral responses to bleaching conditions⁵. Thermal tolerance is shaped by multiple interacting factors including host genetics, the type and plasticity of algal symbionts, associated microbial assemblages, and local environmental histories^{6–8}. Responses to thermal stress can also vary widely with some corals bleaching quickly under even mild warming while others withstand thresholds far beyond predicted values⁹. Corals exposed to frequent but variable thermal stress may be able to acclimatize or adapt, resulting in greater resistance during subsequent warming events, whereas corals in more stable environments may be more vulnerable to the onset of thermal stress^{10,11}.

Hawaiian coral reefs provide an important system for examining these dynamics. In Hawaiian culture, koʻa (coral) is described in the Kumulipo creation chant as the origin of life and ancestral lineage of the Hawaiian people, reflecting a deep genealogical and reciprocal connection between communities and the marine environment¹². This relationship has historically sustained Native Hawaiian communities through fishing and the continued sharing of knowledge of coastal and reef ecosystems. Today, Hawaiian reefs continue to provide critical ecological and economic services, supporting local fisheries

and marine tourism, while also reducing coastal erosion and flood risk by dissipating wave energy along shorelines^{13,14}. Geographic isolation of Hawaiʻi has contributed to relatively low species richness, with fewer than 80 coral species, compared to more than 500 in the broader Indo-Pacific¹⁵. Although species diversity is lower, Hawaiian reefs retain relatively high coral cover dominated by *Montipora*, *Porites*, and *Pocillopora* genera^{16,17}. In some areas, coral cover reaches 30–50%, exceeding levels in other well studied regions such as the Caribbean, where coral cover is often below 13%¹⁸. Despite their abundance, Hawaiian reefs face growing threats from ocean warming, land-based pollution, and coastal development.

Kāneʻohe Bay, located on the eastern coast of Oʻahu, is the largest sheltered embayment in the main Hawaiian Islands. It is one of the most coral dense and well-studied reef systems in the US, and the extensive patch and fringing reef structuring create relatively warm and stable water conditions, with summer surface temperatures frequently exceeding 28°C^{17,19}. These conditions can be favorable for coral growth resulting in high cover but may also heighten vulnerability to thermal stress. In 2014 and 2015, Kāneʻohe Bay experienced mass bleaching events, during which up to 22% of coral cover was lost^{3,20}. Dominant reef building species such as *M. capitata* and *P. compressa* exhibited variable bleaching responses, with some bleaching severely and others remaining healthy^{19,21}. In 2019, another bleaching event occurred and both *M. capitata* and *P. compressa* exhibited moderate declines as compared to more heat-susceptible species²². Recent work suggests that *M. capitata* genotypes in Kāneʻohe Bay differ not only in baseline thermal tolerance but also in their capacity for acclimatization²³. Short-term heat exposure experiments resulted in thermal tolerance enhancement by up to 2-degree heating weeks (DHW) in some colonies while other genotypes showed little to no improvement²³. This within-species variation highlights the presence of resilient genotypes and suggests that prior thermal exposure may be able to prime certain genotypes for enhanced resilience in the future.

Kailua Bay, located just southeast of Kāneʻohe Bay, provides a contrasting reef environment despite its geographic proximity (Fig. 1). Kailua Bay is more exposed to prevailing trade winds and open ocean swell resulting in greater water movement, cooler mean temperatures, and higher physical disturbance²⁴. Seasonal sea surface temperatures range from 22–25°C in winter to 25–28°C in summer, generally cooler than those in Kāneʻohe Bay, where temperatures range from 23–26°C in winter to 27–29°C in summer^{17,24}. This exposure to more variable and cooler conditions may offer thermal buffering, positioning Kailua Bay as a potential climate refuge. Reef structures and coral community compositions also differ between bays. Kailua is characterized by fringing reef flats extending to 5 m depth and seaward reef fronts reaching 20 m. This differs from the shallow fringing, patch, and lagoonal reefs of Kāneʻohe Bay that typically range from 1 to 10 m depth¹⁷. Corals in Kailua are found along spur and groove channels, and hard coral cover is lower than that of Kāneʻohe with reefs mainly consisting of octocorals and turf algae²⁶. Together, these bays provide a natural comparison of adjacent coral communities shaped by distinct environmental regimes.

This study evaluates natural variation in the thermal tolerance of *M. capitata* and *P. compressa* collected from both Kāneʻohe Bay and Kailua Bay (Ulupaʻu). Although both species are widespread and abundant, it remains unclear whether differences in local environmental conditions influence their physiological responses to heat stress. Coral fragments from each bay were exposed to a controlled thermal stress test, and photosynthetic efficiency was quantified using PAM fluorometry. Short-term stress assays of this kind have been shown to predict bleaching susceptibility observed in the field²⁷. By comparing corals from two contrasting reef environments, we tested whether environmental history shapes thermal tolerance and if this pattern is consistent between and within species.

Results

ED30 values ranged from 5.93 to 7.21 eDHW (*M. capitata*: 5.93–7.14 eDHW; *P. compressa*: 6.17–7.21 eDHW; Supplementary Table 1.) There was a significant species-bay interaction ($\chi^2 = 6.55$, $p = 0.010$). Within Kāneʻohe Bay, ED30 values did not differ significantly between species (mean difference = 0.13 eDHW, $p = 0.22$; Fig. 2B). In contrast, at Ulupaʻu, *P. compressa* exhibited significantly higher ED30 values than *M. capitata* (mean difference = 0.65 eDHW, $p = 0.001$; Fig. 2B). ED30 did not differ between bays for *M. capitata* (mean difference = 0.14 eDHW, $p = 0.50$), whereas ED30 was higher at Ulupaʻu than Kāneʻohe Bay for *P. compressa* (mean difference = 0.39 eDHW, $p = 0.012$; Fig. 2B). Variability in ED30 values differed significantly among species and bays ($F_{3,36} = 3.85$, $p = 0.017$), with greater variance in Kāneʻohe Bay than at Ulupaʻu for both species (Supplementary Table 1.)

Bleaching rates (slopes of photosynthetic efficiency) were not significantly related to thermal tolerance thresholds (ED30) ($\chi^2 = 0.56$, $p = 0.46$). However, *P. compressa* bleached significantly slower than *M. capitata* ($\chi^2 = 10.18$, $p = 0.0014$). Within species, slopes did not differ between bays ($\chi^2 = 0.38$, $p = 0.54$), and there was no interaction between ED30 and species ($\chi^2 = 0.80$, $p = 0.37$).

Discussion

Our results demonstrate that environmental history can shape coral thermal tolerance, but responses are species-specific. Both *M. capitata* and *P. compressa* in this study were found to be thermally robust with bleaching thresholds indicated by ED30 values exceeding NOAA's Coral Reef Watch 4 DHW threshold as the level of accumulated heat stress associated with the onset of significant coral bleaching²⁸. Thermal events up to and surpassing 8 DHW have been associated with widespread coral bleaching and mortality *in situ*^{28–30}. Colonies of *M. capitata* in this study ranged from 5.93–7.14 eDHW (mean = 6.44), and *P. compressa* ranged from 6.17–7.21 eDHW (mean = 6.70). Other studies have reported comparable thermal tolerance ranges for Pacific coral species^{31,32}. Both field and experimental studies have reported that *M. capitata* and *P. compressa* can persist through repeated bleaching events in Kāneʻohe Bay, while other native species such as *Pocillopora* experienced higher occurrences of bleaching and mortality under equivalent stress^{19,21}.

Differences in thermal tolerance across species and bays were largely driven by elevated tolerance in *P. compressa* from Ulupa'u. *P. compressa* from Ulupa'u displayed significantly higher thermal tolerance than both Kāne'ohe Bay conspecifics and all *M. capitata* colonies sampled. Oceanic influence at Ulupa'u may contribute to reduced chronic stress exposure by limiting prolonged nutrient enrichment and sustained thermal anomalies^{24,33}. These conditions may favor the persistence of heat-tolerant *P. compressa* genotypes. At the same time, increased flushing can generate greater short-term temperature variability relative to the more thermally buffered conditions of Kāne'ohe Bay. Exposure to such thermal variability may further enhance thermal tolerance, as corals from more variable environments can exhibit increased resilience to heat stress^{34–36}. For example, *Acropora hyacinthus* from fluctuating back reefs survived heat stress better than conspecifics from stable habitats³⁷.

Notably, the two species in this study are demonstrating variable plasticity in thermal tolerance despite being exposed to the same environmental regimes across bays. This suggests that bay alone does not predict thermal performance across taxa. Population genetic studies have shown that both species are generally well connected across reef sites on O'ahu^{38,39}, suggesting that large-scale genomic differentiation is unlikely to fully explain the differences observed here. Instead, variation may arise from differences in gene regulation, protein expression or other physiological mechanisms that influence stress responses without requiring fixed genetic divergence. Increasing evidence suggests that thermal tolerance in corals can be mediated by regulatory plasticity rather than structural genetic differences, with some populations exhibiting differential expression of stress-response pathways when exposed to thermal stress⁴⁰. Recent work has shown that *M. capitata* exhibits expression plasticity in response to thermal preconditioning²³. However, in the present study, *M. capitata* sampled exhibited relatively uniform ED30 values across bays suggesting that while expression plasticity exists, *M. capitata* may operate within a narrower physiological window than *P. compressa*. One possibility is that *M. capitata* possesses inducible stress-response pathways that can be activated through preconditioning but still converge toward a similar upper thermal limit. Previous work has shown that corals exposed to different thermal regimes may exhibit only limited shifts in thermal tolerance and optimal temperatures, suggesting that acclimatization can occur within a constrained physiological range⁴¹. Conversely, *P. compressa* may exhibit greater variability in the magnitude or timing of cellular stress responses across environments, resulting in the tolerance variations observed between bays. This would explain why environment may drive an elevated thermal tolerance response in *P. compressa* but not *M. capitata*.

In some coral species, variation in algal symbiont communities can strongly influence thermal tolerance, with hosting *Durussdinium* often associated with enhanced heat resistance^{5,42}. However, *P. compressa* in Hawai'i is known to form a stable association almost exclusively with *Cladocopium* across a wide range of environments^{42,43}. This suggests that symbiont flexibility is unlikely to explain the enhanced thermal tolerance we observed at Ulupa'u. Future work will examine the potential role of algal endosymbiont communities in shaping thermal tolerance patterns within this system using ITS2 sequencing.

Another factor that could potentially be driving elevated thermal performance of *P. compressa* at Ulupa'u is the differing morphology compared to Kāne'ohe Bay conspecifics. *P. compressa* exhibits morphological plasticity, with growth forms varying across environmental gradients, and these structural differences have been linked to physiological performance and stress resistance^{38,44,45}. In Kāne'ohe Bay, colonies typically display more open branching morphologies, while in the more wave-exposed environment of Ulupa'u, they develop compact, knobby growth forms. The latter morphology may enhance tolerance to thermal stress by increasing tissue thickness, and moderating light exposure due to lower surface area, thereby buffering colonies against bleaching. Morphologies also differed across bays for *M. capitata* with colonies from Ulupa'u exhibiting more of a plating morphology compared to Kāne'ohe's branching morphology. Morphological differences observed in *M. capitata* across bays may not necessarily indicate underlying genetic or phenotypic variation. Coral morphology is highly phenotypically plastic, and recent work has shown that *M. capitata* can exhibit environmentally driven shifts in colony form under varying light regimes⁴⁶.

Within Kāne'ohe Bay, *P. compressa* and *M. capitata* colonies from all three collection sites exhibited similar levels of thermal tolerance. The population genetic structure of *M. capitata* within Kāne'ohe Bay aligns with environmental mosaics, suggesting that local selective pressures may drive differentiation within the bay⁴⁷. Surprisingly, our results did not detect significant differences in thermal tolerance among Kāne'ohe sites for either species. This apparent uniformity may be due to homogenizing forces such as shared heat exposure histories resulting in similar tolerance across the bay. Despite similar mean values, variability in ED30 was significantly greater in Kāne'ohe Bay than at Ulupa'u for both species, which may reflect the environmental heterogeneity of the three collection sites within Kāne'ohe Bay. Repeated bleaching events in Kāne'ohe Bay (1996, 2014, 2015, 2019) may have also filtered out the most heat-sensitive genotypes, leaving a pool of remaining coral colonies with uniformly higher tolerance while still preserving some level of variation among colonies. Together, these results suggest that while average thermal tolerance appears consistent across Kāne'ohe sites, the distribution of tolerance within populations remains relatively broad.

Despite ecological contrasts across bays, both species exhibited substantial thermal tolerance, with ED30 values consistently exceeding the 4 eDHW threshold. The contrasting patterns observed between *M. capitata* and *P. compressa* show that the capacity to acclimatize or express elevated thermal tolerance is not uniform across species even within the same reef systems. This shows that resilience in one coral species does not necessarily predict resilience in another, even when they share similar habitats and exposure histories. From a restoration perspective, populations that consistently exhibit high thermal tolerance, such as *P. compressa* from Ulupa'u, may be attractive candidates when immediate resistance to heat stress is a management priority. However, prioritizing the highest thermal tolerance alone, without consideration of underlying genetic diversity, may increase the risk of genetic bottlenecks and limit long-term adaptive capacity. Conversely, sourcing individuals from populations with greater within-site variability in thermal tolerance may incorporate both thermally resilient and sensitive genets but would preserve genetic diversity and adaptive potential. Importantly, results from

this work reinforce that both *M. capitata* and *P. compressa* corals, across multiple habitats, contain genets of high thermal tolerance. These results underscore the value and need for species-specific and region-specific approaches to reef restoration and management efforts in Hawaiʻi.

Methods

Coral Collection and Site Selection

Coral fragments were collected from four sites on Oʻahu, Hawaiʻi: three within Kāneʻohe Bay (December 2023) and one in Ulupaʻu in Kailua Bay (April 2024) (Fig. 1A). Site selection within Kāneʻohe Bay was informed by hydrodynamic studies⁴⁸ that defined spatial patterns in water residence time and flow, and by known environmental gradients in temperature, turbidity, and wave exposure⁴⁹. The Ulupaʻu site was included to provide a broader geographic and environmental context for comparison across reef systems. At each site, we sampled 10 fragments from each of 5 colonies of *M. capitata* and 5 colonies of *P. compressa* ($n = 10$ colonies per site, 40 total). These species have low rates of clonality in Kāneʻohe Bay, so we enforced a minimum distance of 10 m between colonies to avoid collecting clones. Collected corals were transported to the Hawaiʻi Institute of Marine Biology (HIMB), fragmented, trimmed to ~ 5 cm branches, affixed to calcium carbonate plugs, and transferred to an *in situ* common garden nursery at Reef 13 for recovery. Corals remained in nursery until June 2024, then were brought back to HIMB to undergo thermal performance testing.

Thermal Performance Test

To assess thermal performance, two fragments per colony ($n = 40$ colonies $\times$ 2 fragments = 80 total fragments) were exposed to a controlled heat-stress assay in flow-through mesocosms at HIMB using similar methods as described in Replicates were distributed across two independent experimental tanks, with one fragment per colony placed in each tank to control for potential tank effects. Temperature was continuously logged using in-tank temperature loggers, and photosynthetically active radiation (PAR) was recorded with dedicated loggers in each tank to monitor light conditions.

For stress testing, temperatures increased from 25.5°C to 32.0°C at a ramp rate of 1°C per day over six days, reaching a maximum of 32°C, corresponding to 4°C above the region's maximum monthly mean. Temperatures were then held at 32°C for the remainder of the experiment (Fig. 1B). Photosynthetic efficiency was measured using a Walz Imaging-PAM Chlorophyll Fluorometer approximately one hour after sunset, including two days of baseline measurements immediately prior to the onset of the thermal ramp and every two days during the experiment (Fig. 1B). Corals were dark acclimated for one hour prior to each reading to ensure full relaxation of PSII reaction centers and accurate assessment of maximum quantum yield (F_v/F_m). For each fragment, three F_v/F_m values were recorded and averaged for downstream analysis.

Data Analysis

Temperature and PAM fluorometry data processing followed approaches adapted from Drury et al. (2022). After confirming that tank did not significantly impact F_v/F_m trajectories, data from each tank were averaged together for subsequent analyses. To quantify continuous thermal tolerance, we used dose response modeling of relative F_v/F_m against eDHW in the R package `drm`⁵⁰ and extracted various effective doses following Drury et al. 2022. We averaged replicate F_v/F_m values for each genotype at each timepoint and relativized them to the baseline F_v/F_m (collected before the temperature ramp). Experimental degree heating weeks (eDHW) were computed following Leggat et al. 2022⁵¹, using 27.5°C as the MMM based on long-term NOAA Coral Reef Watch climatology for Kāneohe Bay. Based on observed declines, we selected ED30 as a standardized endpoint metric of thermal tolerance, representing the cumulative heat exposure at which colonies experienced a 30% reduction in photosynthetic efficiency.

ED30 values were analyzed using a generalized linear mixed-effects model (GLMM) implemented in the package `glmmTMB`⁵², with species, bay, and their interaction included as fixed effects and site nested within bay as a random effect. Significance of model terms was evaluated using Type II Wald χ^2 implemented in the `car` package⁵³. Post hoc pairwise comparisons were conducted using estimated marginal means in the R package `emmeans`⁵⁴. Variability in ED30 within sites and across bays was assessed using Levene's tests for homogeneity of variance.

To test whether the bleaching rate (slope) of F_v/F_m decline was related to thermal tolerance (ED30), we fit a GLMM with slope as the response and ED30, species, bay, and their interaction as predictors. Site nested within bay was included as a random effect. Effects were evaluated using Type II Wald χ^2 tests. All analyses were conducted in R (v4.4.2)

Declarations

Competing Interests

The authors declare no competing interests.

Funding Declaration

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Author Contribution

C.D., K.H, R.T., J.D.V, and A.M.K. conceived and designed the study. K.H. and R.T. acquired permits. C.D., R.T., and J.D.V. acquired funding. A.M.K. wrote the first draft of the paper; A. M. K., J.R.H, C. J. L, J. L., K. H., C. D., R. T., and J. D.V. critically revised the manuscript.

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Data Availability

All data generated or analyzed during this study are included in this published article and its Supplementary Data files. Code to reproduce the analyses presented in this paper and data files needed for such reproduction may be found on [https://github.com/Allison-Klein/K2K_NaturalVariationManuscript](https://github.com/Allison-Klein/K2K_NaturalVariationManuscript)

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Figures

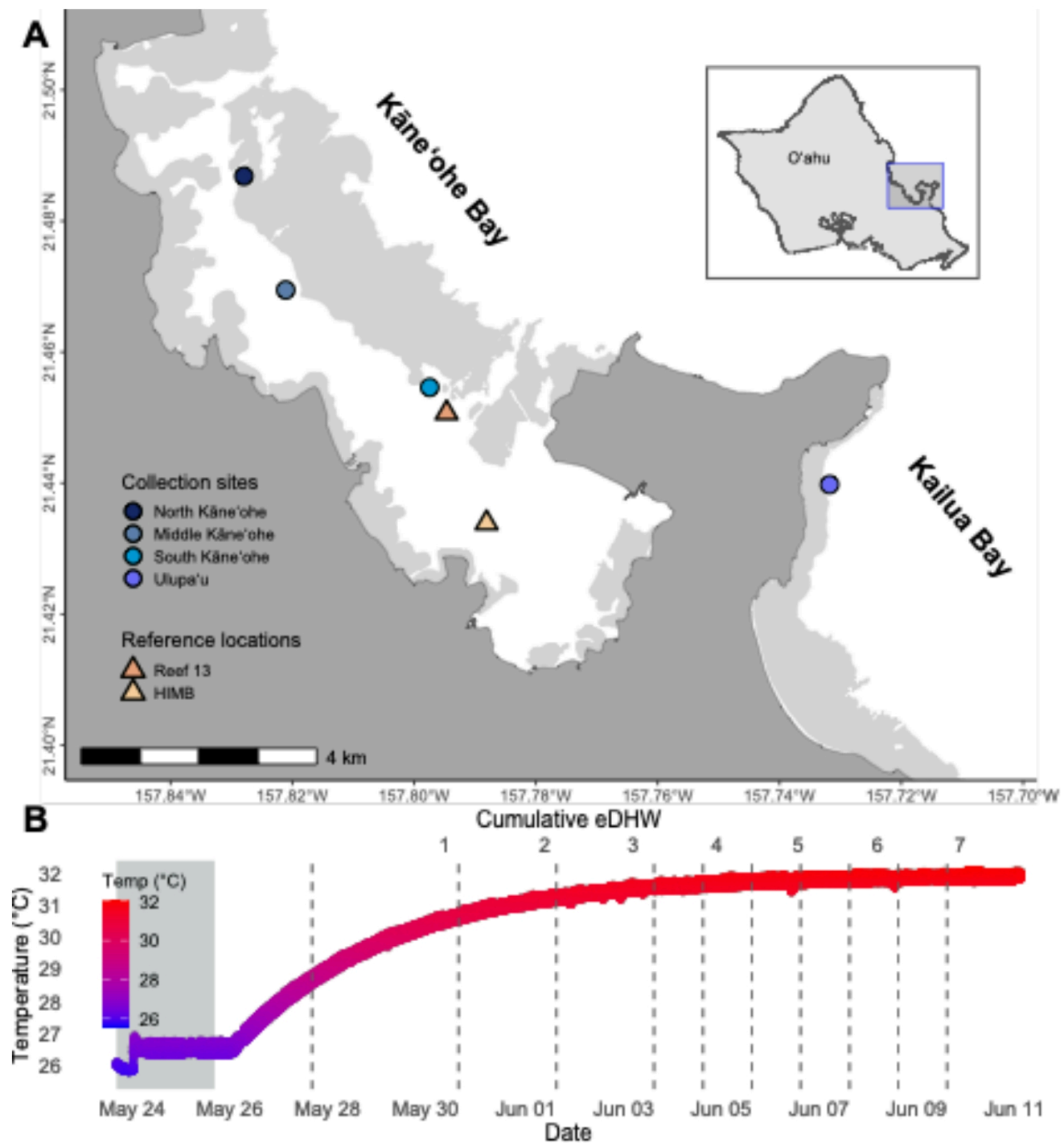


Figure 1

(A) Coral collection sites within Kāneʻohe Bay ($n = 3$; North Kāneʻohe, Middle Kāneʻohe, and South Kāneʻohe) and Kailua Bay ($n = 1$; Ulupaʻu). Reef 13, located near HIMB, served as the Kāneʻohe nursery and transplant site. The **light grey** regions within Kāneʻohe and Kailua Bays represent **coral reef habitats and shallow reef structure**. (B) Raw experimental tank temperature profile during thermal stress assay. The shaded region marks the baseline period during which initial PAM fluorometry measurements were

collected prior to thermal ramp. Dashed vertical lines correspond to subsequent PAM sampling days. The upper x-axis shows cumulative eDHW calculated from tank temperatures.

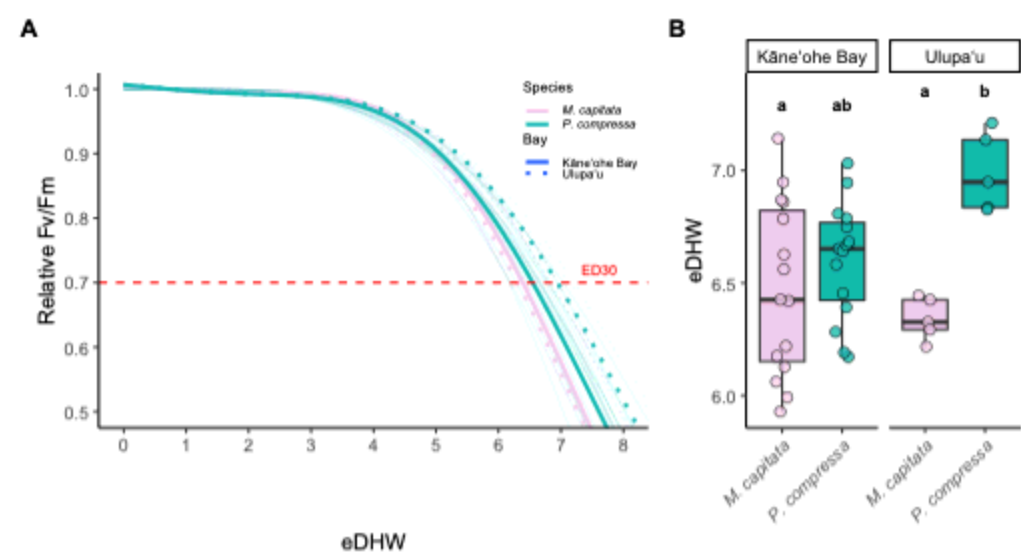


Figure 2

Thermal performance of *M. capitata* and *P. compressa* across bays. (A) Trajectories of relative declines in F_v/F_m under cumulative heat stress (eDHW). Lines represent species (color) and bay (line type) level means, with faint lines representing induvial colonies. The dashed red line represents a 30% decline in F_v/F_m . (B) Box plots showing ED30 for each species from Kāneʻohe Bay and Ulupaʻu. Boxes summarize the distribution of colony-level ED30 values, center lines indicate medians, and points represent individual colonies. Letters above boxes denote significant differences among groups (Tukey-adjusted, $p < 0.05$).

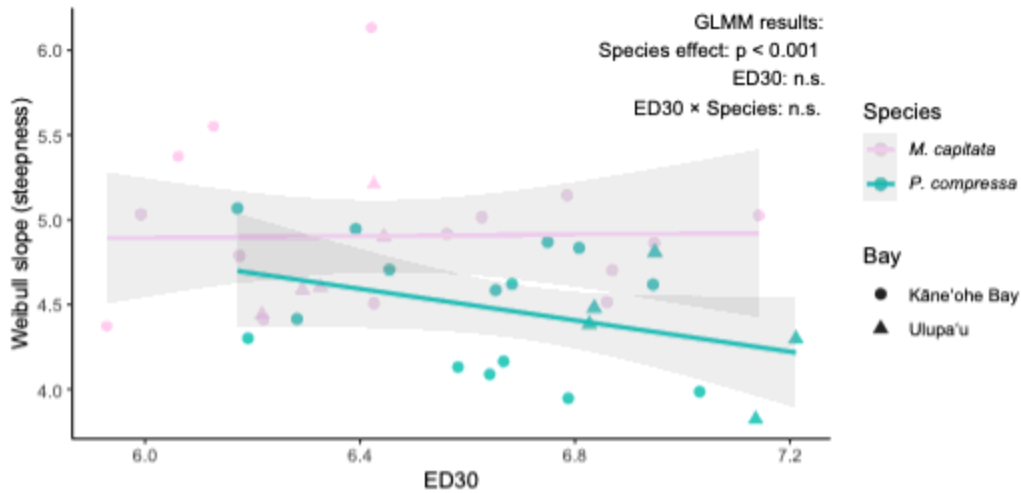


Figure 3

Relationship between ED30 and Weibull slope steepness for each species. Points represent colonies (shaped by bay), and lines show species specific linear fits with 95% CI. GLMM results are shown on plot.

Supplementary Files

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