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Extirpation of *Acropora cervicornis* genotypes from a coral nursery during the 2023 marine heatwave undermines conservation efforts

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Global climate change has decimated historical baseline coral cover in the Caribbean, including wild *Acropora cervicornis*, now listed as Critically Endangered by the IUCN Red List of Species. Although still at risk to the same environmental conditions that decimated wild populations, propagating *A. cervicornis* genotypes with increased disease resistance and thermal tolerance could help prevent extinction. Here we document the impacts of the 2023 marine heatwave on the health and survival of nursery reared *A. cervicornis* corals in Little Cayman that experienced 19.4 Degree Heating Weeks (DHW). In total, 91.6% of the 415 colonies suffered complete mortality with seven out of ten genotypes being eradicated, suggesting a genetic basis for thermotolerance. This accentuates the importance of genetic diversity for survival of *A. cervicornis*. However, the eradication of over 90% of coral colonies also highlights the futility of putting corals back into the same environment, emphasizing the need for innovative conservation strategies that incorporate novel tools capable of enhancing resilience and ensuring restoration remains viable under future climate conditions.

KEYWORDS

coral bleaching, survival, restoration, climate change, global warming, thermal tolerance, Caribbean, Little Cayman

Introduction

The rapid increase of natural and anthropogenic stressors on Caribbean coral reefs is threatening the capacity of corals to grow, survive and create reef ecosystems (Pandolfi et al., 2003; Hoegh-Guldberg et al., 2007; Hughes et al., 2017; Donovan et al., 2021). Over the past 50 years, the region has undergone dramatic declines resulting in current coral cover less than 50% of historical records (Gardner et al., 2003; Jackson et al., 2014). Scleractinian corals live close to their maximum temperature tolerance, and thus an

increase in temperatures of just 1°C can result in expulsion of their photosynthetic algal symbionts, referred to as bleaching (Brown et al., 2002; Suggett and Smith, 2011, 2020). As many corals rely on their algal symbionts to meet most of the energetic needs, this dysbiosis can ultimately lead to starvation and mortality.

The historical loss of corals in the Caribbean and across the globe has led to many initiatives aimed at restoring threatened coral species, such as the staghorn coral, *Acropora cervicornis*. Previously a dominant coral species on shallow Caribbean reef systems, *A. cervicornis* experienced significant loss in the early 1980s due to an outbreak of white band disease (Aronson and Precht, 2001, 2006) and continues to decline in abundance with subsequent disease and bleaching events (Gardner et al., 2003) leading to its listing as critically endangered by the IUCN under criteria A2bce (Crabbe et al., 2022). As the main branching species in the region, this decline led to a loss of complexity on the reef, depriving reef biodiversity from hiding spots, feeding, and growing surfaces (Agudo-Adriani et al., 2016). Currently, *A. cervicornis* is the most common species used in restoration efforts in the Caribbean, representing roughly 30% of restoration projects (Boström-Einarsson et al., 2020). However, a major hurdle to restoration success has been survival post outplanting, primarily driven by continued outbreaks of white band disease and thermal anomaly events (Hughes et al., 2023). This has led many restoration practitioners to explore the potential for rearing disease resistant and temperature tolerant individuals to increase restoration success (Oppen et al., 2015; Quigley, 2024).

Coral thermotolerance, or the ability of corals to withstand higher temperatures, is a crucial factor in their survival in the face of rising ocean temperatures. Through different mechanisms, a colony can prove resilient to heat stress to some extent. First, acclimatization allows corals to adapt to higher temperatures over time enabling them to tolerate heat stress (Sawall et al., 2015; DeCarlo et al., 2019) often achieved by shuffling symbiont species (Baker et al., 2004; Quigley et al., 2019; Karp et al., 2025). However, since *A. cervicornis* primarily hosts a single species of Symbiodiniaceae and does not experience symbiont shuffling, thermotolerance is likely more strongly driven by the host genome (Muller et al., 2018; Indergard et al., 2022). Second, tolerance may be inherited from parent colonies that experienced heat stress through epigenetics (Eirin-Lopez and Putnam, 2019). Evidence of epigenetics has been shown by several studies on acroporid species reporting changes in DNA methylation patterns associated with heat stress that could underlie the intergenerational transfer of thermal tolerance or phenotypic plasticity to environmental stress (Hazraty-Kari et al., 2022; Hackerott et al., 2023; Guerrero and Bay, 2024). Third, variations in host genetic composition or gene expression response may result in higher temperature tolerances among individuals within a population (Bellantuono et al., 2012; Jin et al., 2016; Kenkel and Matz, 2016; Yetsko et al., 2020; Karp et al., 2025). For example, Jin et al. (2016) identified specific genetic markers in *Acropora millepora* that were linked to differences in responses to environmental stress, providing evidence for a genetic basis of thermal tolerance. Thus, recent efforts focus on maintaining high genetic diversity and/or manipulating

genetic composition of nursery reared corals to achieve higher rates of survival under increased thermal stress (Kiel et al., 2023).

In 2023, the Cayman Islands experienced an unprecedented marine heatwave with water temperatures surpassing 32°C and sustained above 31°C for several weeks. These high temperatures corresponded to an estimated 19.4 Degree Heating Weeks (DHW), a metric representing accumulated heat stress that is calculated based on the rolling sum of the number of weeks for which the sea surface temperature has exceeded the maximum mean monthly temperature accumulated over the preceding 12 weeks by at least 1°C (Gleeson and Strong, 1995; Liu et al., 2013). This excessive heating event led to widescale coral bleaching and mortality across the fore-reef zone in Little Cayman and across the Caribbean (Goreau and Hayes, 2024; Reimer et al., 2024; Doherty et al., 2025; Goodbody-Gringley and Chequer, 2025). Concurrently, this heatwave affected the *A. cervicornis* colonies growing in a nursery maintained by the Central Caribbean Marine Institute (CCMI), which contained individuals of known genetic identity. This event, therefore, served as an occasion to study thermal tolerance differences among genetically diverse nursery reared individuals in response to a natural heatwave. Using recurrent underwater bleaching and survival surveys along with continuous temperature measurements throughout the thermal stress event, we document critical points in the survival of *A. cervicornis* and identify specific genotypes with higher thermal tolerance. Understanding the effects of marine heatwaves on a genetically diverse population is the key to successfully restore and repopulate impacted reefs. Moreover, establishing DHW's thresholds will improve our ability to predict the impacts of future heatwave events on the persistence of coral reefs.

Materials and methods

Study site and data collection

This work took place in CCMI's *A. cervicornis* nursery on the north coast of Little Cayman Island that was originally established in 2012 (19.329858, -81.252361; Figure 1A). The nursery is located on the northern side of Little Cayman, roughly 700m from shore at a depth of 16 – 18m (Figure 1B). All corals maintained in the nursery were collected from wild colonies around the island between 2012 and 2018. At the onset of the study the nursery contained 415 *A. cervicornis* individuals, which represented 10 unique genetic identities (Drury et al., 2017; Brown et al., 2022), referred to hereafter as genotypes B, G, K, LG, O, OB, OR, R, S, and Y, dispersed among 11 vertical frames (Figure 1C). Frames were 3-m wide by 1.5-m high and constructed of PVC with corals hanging from horizontal monofilament lines. The structures were anchored using ropes tied to cinderblocks and held upright by empty plastic jugs partially filled with compressed air. Frames were ~1–3 m away from any other frame, and each contained a minimum of 3 different genotypes.

Health surveys began on June 30, 2023, and were conducted approximately every two weeks thereafter, until January 6, 2024. On each survey, individuals were assigned a visual health status of Diseased, Healthy, Missing, Partially Alive or Dead, and a bleaching

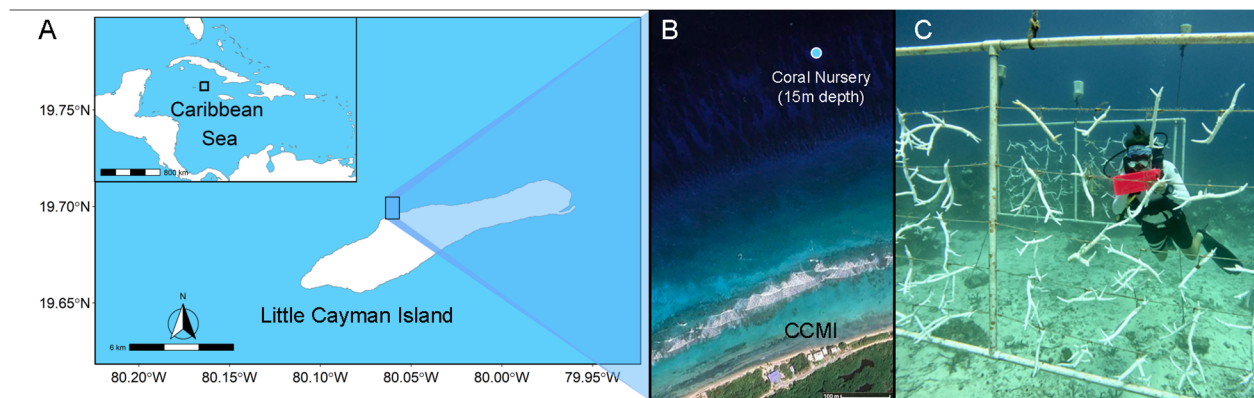


FIGURE 1

(A) Map of Little Cayman within the Caribbean and position of the nursery on the north shore. (B) The inset displays the position of the coral nursery on Little Cayman. (Imagery (c)2025 Airbus, CNES / Maxar Technologies, Map data (c)2025). (C) Image of the nursery during the peak of the heatwave showing fully bleached colonies.

status of Bleached, Partially Bleached and Not Bleached. Routine nursery maintenance also occurred on each survey dive.

Seawater temperature was recorded using Onset HOBO Water Temperature Pro v2 Data Loggers secured to the top of a frame at 15m depth, on the mooring line at 10m depth, and at the surface below the mooring buoy. Temperature was recorded every minute from July 18, 2023, through January 6, 2024. Degree Heating Week data was taken from the Coral Reef Watch website (NOAA Coral Reef Watch, 2014, updated daily), which is updated daily by the National Oceanic and Atmospheric Administration (NOAA).

Statistical analysis

Statistical analyses were conducted on R version 4.1.0 (R Core Team, 2023). Temperature was compared among logger deployment depths (satellite surface, *in situ* surface, 10m, 15m) using a non-parametric Kruskal-Wallis' tests, as they did not meet the assumption of normality. *Post hoc* analysis was conducted using a Dunn's test in the FSA package (Ogle et al., 2025).

The impact of genotype on colony status was assessed using a generalized linear model (GLM) with a Poisson distribution, implemented via the lme4 package in R. The response variable was the count of live colonies per genotype, and the fixed effect was genotype. Sampling date (recorded as day/month) was included as a random effect to account for temporal variation in survivorship. A Poisson distribution was chosen due to the count-based nature of the data, which included no negative values. Prior to model fitting, we assessed assumptions of the Poisson distribution, including the potential for overdispersion, using residual deviance and dispersion tests. No significant overdispersion was detected, justifying the use of the Poisson GLM.

To estimate and visualize survival probabilities over time, Kaplan-Meier survival curves were generated (Kaplan and Meier, 1958) using the survival package (Therneau, 2024). Survival curves were generated separately for each genotype, and differences between curves were evaluated using a Log-rank test with Bonferroni correction for multiple

comparisons. Sample sizes per genotype ranged from 10 to 149 and were consistent across analyses.

A dissimilarity matrix was constructed to quantify differences in survival patterns between genotypes. This matrix was derived solely from the pairwise p-values of the Log-rank tests, using the formula: $\text{dissimilarity matrix} = 1 - \text{Log rank test } p\text{-value}$. These values represent inverse similarity in survival between genotypes, such that higher values indicate greater divergence. The matrix was used for hierarchical clustering using the average linkage method, implemented via the hclust function in R. This approach enabled visualization of genotype groupings based on survival divergence across the monitoring period. Only survival data were included in this matrix. All survival data were cumulative across the full monitoring period, rather than separated by date.

Results

Temperature

Seawater temperature differed significantly among the temperature measurements obtained via satellite and *in situ* loggers at the surface, 10m, and 15m depth (chi-squared = 364, $p < 0.001$). Surface temperature recorded by the *in situ* logger was significantly higher than the sea surface temperature registered by NOAA ($z = -18.714496$, $p < 0.001$), with the highest temperature recorded at the surface by the *in situ* logger at $33.5 (\pm 0.01)^\circ\text{C}$ on October 8, 2023 (Figure 2). Because *in situ* temperature loggers were deployed midway through the heatwave, coral responses were interpreted using NOAA's DHW values, which is supported by the strong agreement between temperature records in the nursery (15m depth) and satellite-derived sea surface temperatures.

Observational health response

The first signs of bleaching were observed on August 30, 2023, when DHW values rose from 4.5 to 11.6 (Figure 3). At this time,

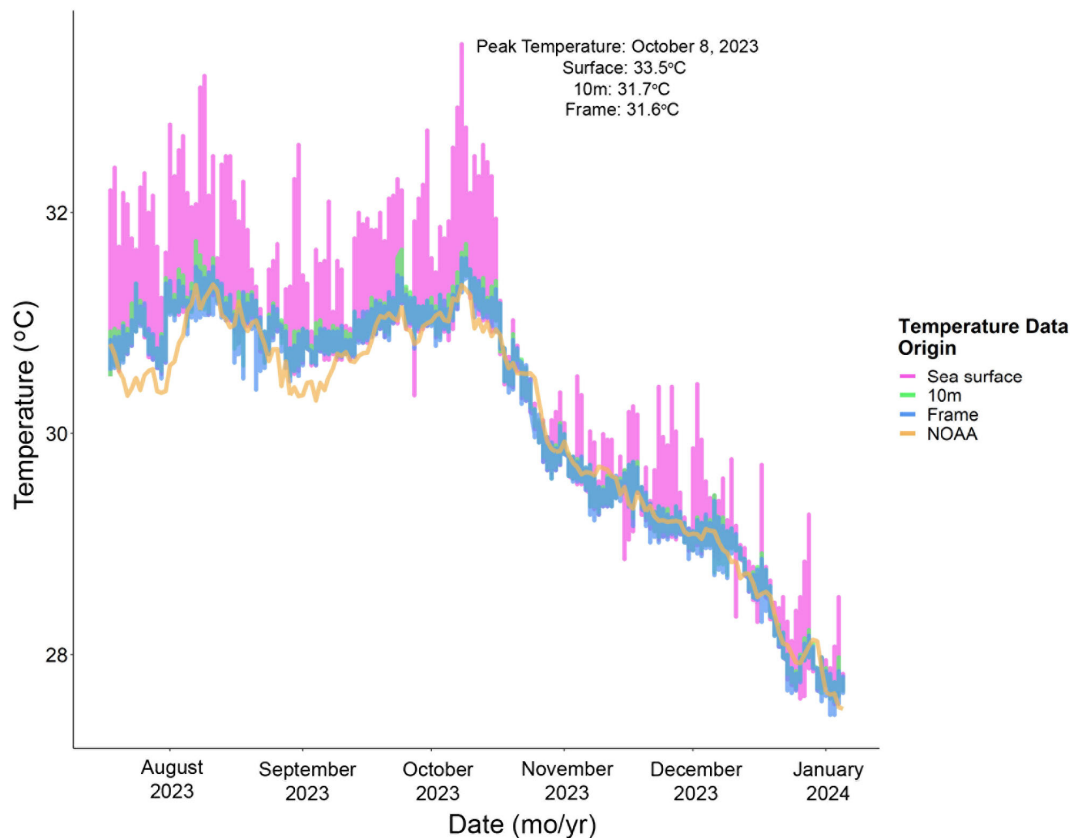


FIGURE 2

Seawater temperature data recorded from HOB0 loggers at the sea surface (pink), 10m depth on the nursery mooring line (green), and 15m depth on a nursery frame (blue). The orange line depicts estimated SST from the NOAA Coral Reef Watch Virtual Stations monitoring. *In situ* temperature data began on July 18, 2023 and ended on January 6, 2024.

94.9% (394 colonies) showed signs of bleaching, including 6.9% (29) that were fully bleached, 1.7% (7) dead, and 3.4% (14) remaining healthy. By September 16, 2023, 81.9% (340 colonies) were fully bleached, 6.7% (28) partially bleached, and mortality had increased to 7.7% (32 colonies). The number of healthy colonies remained stable at 3.6% (15). DHW peaked at 19.44 on October 16, 2023. At that point 91.6% (380 colonies) were dead, 2.9% (12) were fully bleached, and 5.5% (23) were partially bleached – no healthy colonies remained. The increase in both bleached ($z = -17.332$, $p < 0.001$, GLM) and dead colonies ($z = -2.205$, $p = 0.027$, GLM) was significantly associated with rising DHW when accounting for date. As temperatures declined, some recovery was observed. By November 23, 2023, only 3 colonies remained partially bleached (0.7%), while 20 colonies (4.8%) appeared fully recovered. At the final survey on January 6, 2024, 18 colonies (4.3%) were alive and healthy.

Genotypic variability

The full interactive model (date x genotype) revealed a significant effect of genotype on survival ($F = 19.15$, $p < 0.001$, GLM), with genotypes O and OB surviving significantly better than

genotype G ($p < 0.001$ for both). The first mortalities due to bleaching occurred in genotypes G, K, OR, and Y by September 6, 2023, with 3, 11, 6, and 5 individuals lost respectively. By the next survey, additional losses occurred across nearly all genotypes except O. By October 30, 2023, all individuals of genotypes B, G, K, LG, R, S, and OR were dead. At the final survey (January 6, 2024), 18 colonies remained: 7 from genotype O (which only suffered losses before the heatwave), 7 from OB (7/15, 47%), 4 from Y (4/35, 11%) (Figure 4). A fitted Random effect model comparing the percent survival by genotype over time confirmed significant differences between OB and all the other genotypes except O (Tukey *post-hoc*, Table 1, Figure 4). Genotype O differed significantly only from OR.

Kaplan Meier curves showed that survival probability remained relatively stable for ~100 days into the heatwave. Only genotypes OB and R exhibited any survival beyond 200 days, with no genotype exceeding a 50% survival probability. Genotype OB had a 44.4% survival probability at day 197; genotype R had 6.6% survival probability at day 157. Both genotypes were predicted to reach complete mortality by day 225 (Figure 5).

Hierarchical clustering of genotypes based on survival dissimilarities revealed distinct groupings (Figure 6). Genotype OB, which suffered the lowest mortality, formed its own distinct cluster. The remaining genotypes grouped into two main clusters:

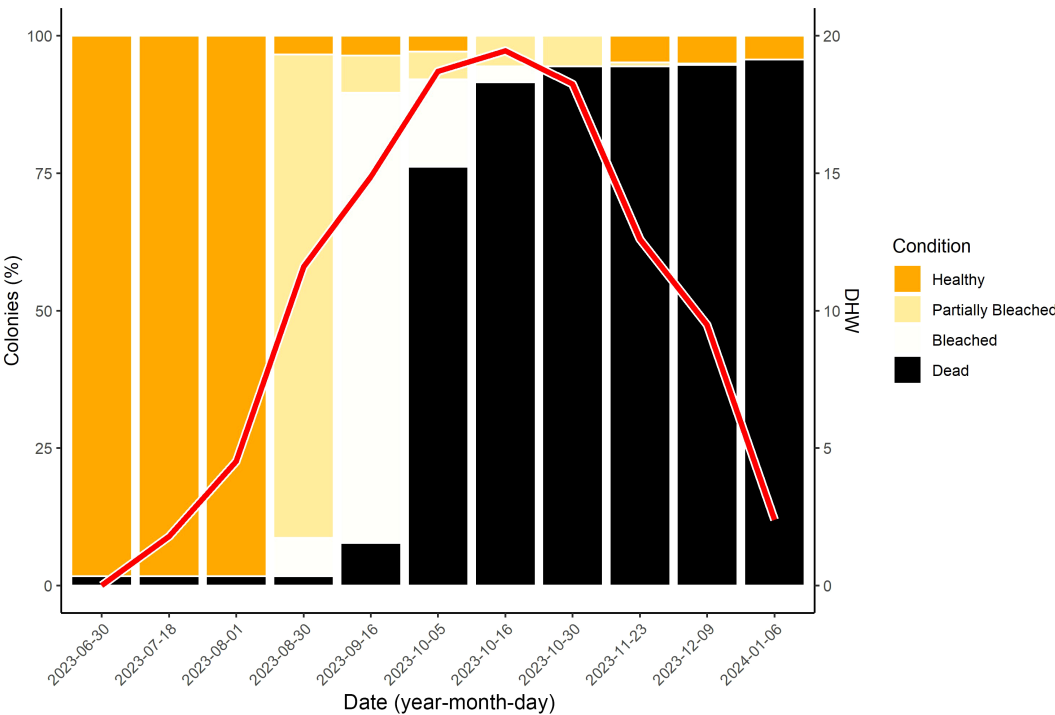


FIGURE 3
Stacked bar plot of coral conditions (Healthy, Partially Bleached, Bleached, Dead) over the sampling period. The solid red line represents estimated DHW from the NOAA Coral Reef Watch virtual stations during the sample period, with DHW values depicted on the Z-axis.

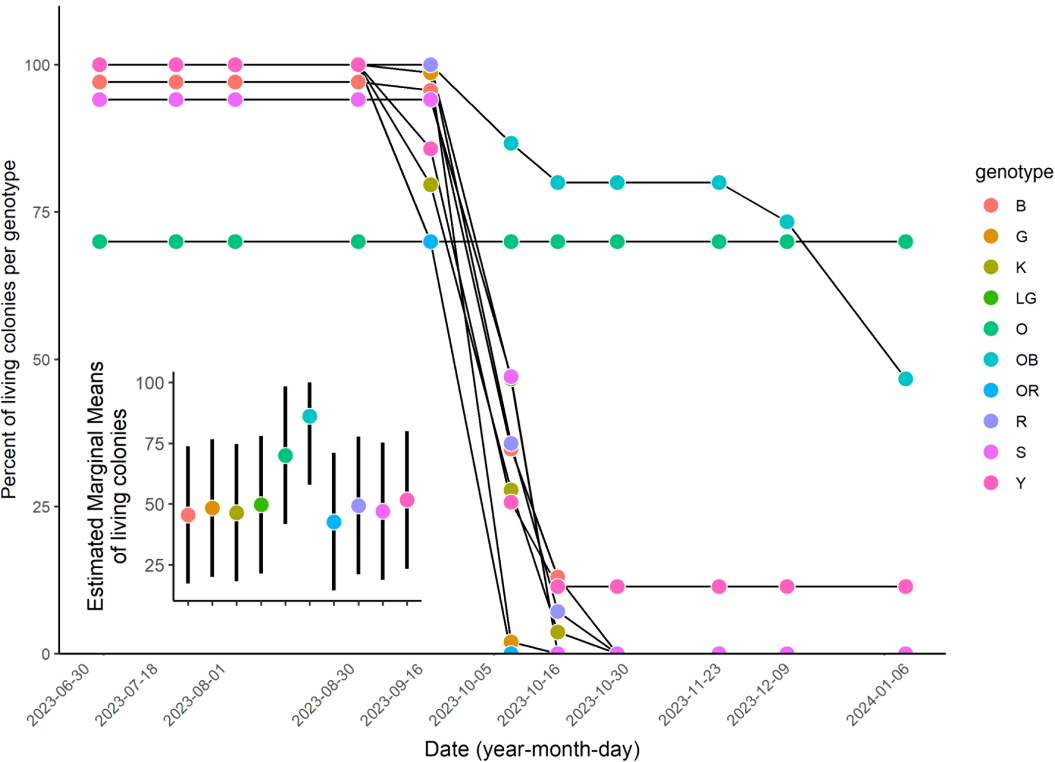


FIGURE 4
Percent survival of colonies by genotype over the monitoring period from June 30, 2023, to January 6, 2024. Inset: marginal mean survival by genotype estimated by the Generalized Linear Model (GLM).

TABLE 1 Pairwise comparisons of the estimated marginal mean survival by genotype (Tukey *post-hoc* method) where light blue represent $p < 0.05$ and purple $p < 0.01$.

| Genotype | G | B | K | LG | O | OB | OR | R | S |
|----------|--------|--------|--------|--------|--------|--------|--------|---|--------|
| G | | | | | | | | | |
| B | 1 | | | | | | | | |
| K | 1 | 1 | | | | | | | |
| LG | 1 | 1 | 1 | | | | | | |
| O | 0.87 | 0.1967 | 0.1161 | 0.2743 | | | | | |
| OB | 0.0001 | 0.0004 | 0.0002 | 0.0008 | 0.6079 | | | | |
| OR | 1 | 0.9995 | 1 | 0.9972 | 0.0342 | <.0001 | | | |
| R | 1 | 1 | 1 | 1 | 0.2526 | 0.0007 | 0.9981 | | |
| S | 1 | 1 | 1 | 1 | 0.1381 | 0.0002 | 0.9999 | 1 | |
| Y | 0.9989 | 1 | 0.9997 | 1 | 0.4189 | 0.002 | 0.9824 | 1 | 0.9999 |

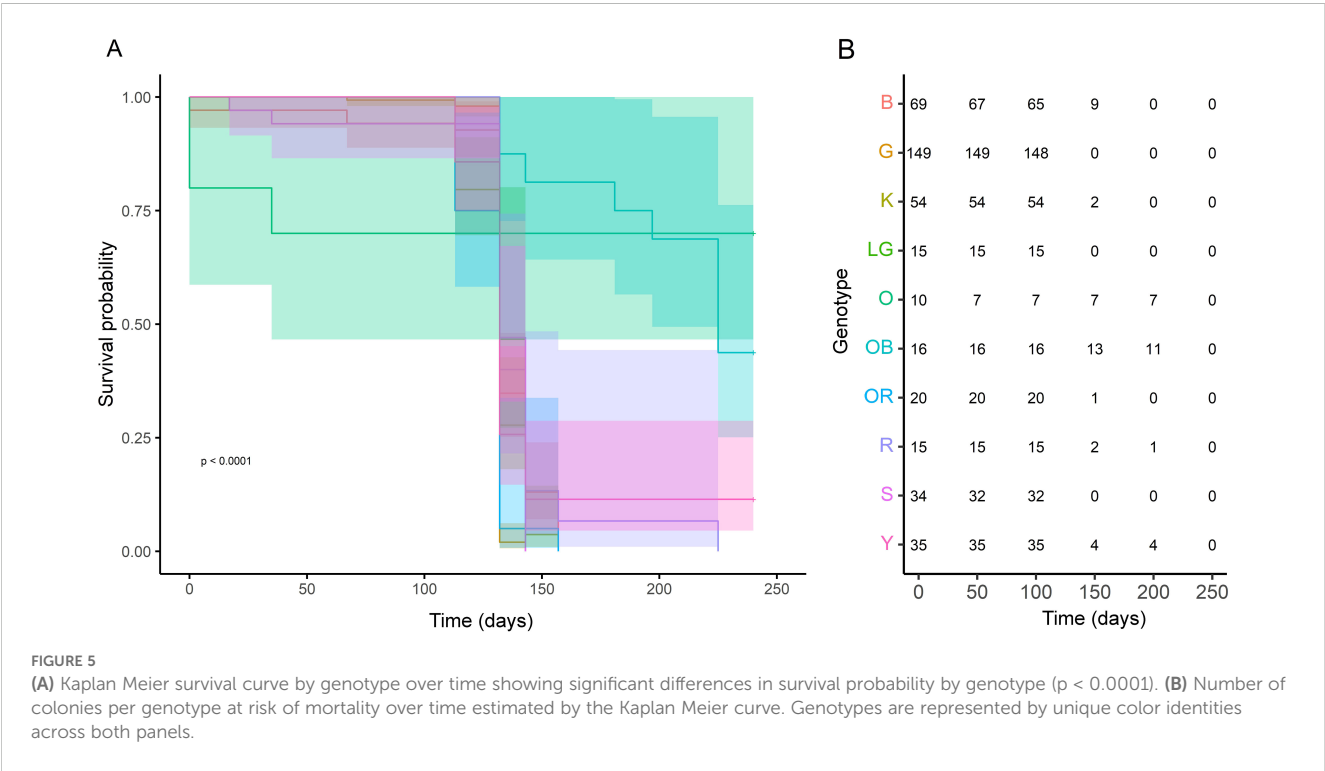
one containing Y, O, R and S, and another divided into two sub-clusters of G and K, and LG and OR.

Discussion

Our results document the devastating impacts of an extreme heatwave to the potential success of *in situ* coral propagation for restoration. All the *A. cervicornis* individuals in our nursery experienced bleaching at the 10 DHW point, and mass mortality occurred by 15 DHWs. At the end of our surveys, 96% of the colonies had suffered mortality after experiencing 19.4 DHWs. Out of the 10 genotypes present at the start of the heatwave, only 3

survived and only a single genotype (O) escaped any heat related casualties. Variations in density of each genotype within the nursery was representative of availability within the overall wild population, and thus these results could have even larger implications on the regional population scale. For example, genotypes B, G, and K, were the most abundant at the start of the heatwave with 69, 149, and 54 fragments in the nursery, representing 66% of the nursery corals, all of which suffered complete mortality. In contrast, genotype (O) was the least abundant at the start of the heatwave, with only 10 fragments, representing 2.4% of the nursery, yet suffered the least mortality.

Despite the dramatic bleaching response witnessed across the nursery in 2023, the variation in bleaching and survival found



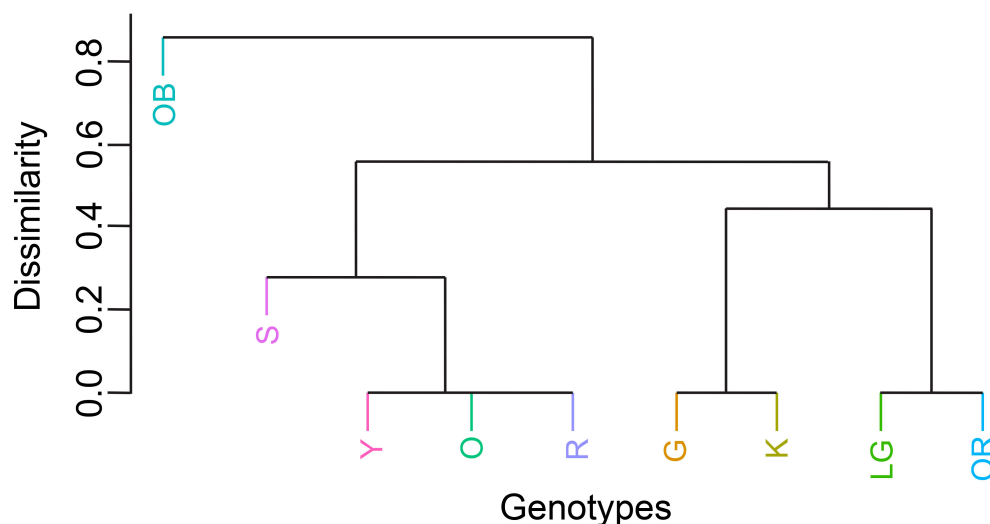


FIGURE 6

Hierarchical cluster comparing the degree of dissimilarity among genotypes, where genotypes clustering together had similar patterns of survival response to the heat wave. Genotypes on isolated and/or distant branches showed significantly different survival patterns.

among genotypes suggests that a genetic basis of thermotolerance exists within this population. Specifically, genotypes O and OB proved to have higher thermal tolerance than all other genotypes, while genotypes K, OR, and Y were the first to suffer from bleaching induced mortality, indicating lower thermal tolerance. Likewise, the Kaplan-Meier curve, indicates that genotype plays a significant role in response to increasing DHWs. In a similar *in situ* study, Ladd et al. (2017) found significant differences in survival among *A. cervicornis* genotypes in a restored population after exposure to 17 weeks above 30°C in the Florida Keys. Thermal history has been shown to impact thermal tolerance in *A. cervicornis*, where individuals with prior exposure to heat stress exhibit higher tolerance to a subsequent stress event (DeMerlis et al., 2022; Indergard et al., 2022). However, the corals in this study had been maintained for over five years in a common-garden nursery at a narrow depth range (15–18 m) with uniform temperature conditions, suggesting that thermal history did not contribute to the observed differences in bleaching and survival among genotypes. Genotype-environment interactions are critical to consider for the success of restoration as genotypes of *A. cervicornis* have been found to differ in disease resistance (Vollmer and Kline, 2008; Brown et al., 2022), growth rates (Griffin et al., 2012; Drury et al., 2017), habitat production (Ladd et al., 2017), and thermal tolerance (Drury et al., 2017; Ladd et al., 2017; Yetsko et al., 2020; this study). For example, Brown et al. (2022) found differences in disease susceptibility among genotypes within the same coral nursery examined here, where genotype G was disease resistant, while genotype K was highly susceptible to disease. Thus, maintaining a high degree of genetic diversity may serve as a vital bet-hedging strategy against environmental stress and climate change-induced losses, making it essential for safeguarding coral restoration efforts. Mechanisms such as assisted evolution to cross-breed thermally tolerant individuals and inoculation with thermally tolerant Symbiodiniaceae species

may further enhance coral resilience and survival under future ocean warming scenarios, improving restoration success (Baums et al., 2019; Nitschke et al., 2024; Karp et al., 2025).

As global temperatures continue to rise, so too does the frequency, intensity, and duration of coral bleaching events. The first widespread bleaching event to affect the Caribbean was documented during the 1982–83 ENSO event (Glynn, 1984; Lasker et al., 1984), with the first global bleaching event occurring in 1998 impacting coral cover across all tropical locations (Goreau et al., 2000; Glynn et al., 2001; Aronson et al., 2002; Wilkinson, 2004). A subsequent global bleaching occurred in 2010, followed just four years later by another ENSO driven event spanning 2014–2016 that was the most severe and widespread bleaching event ever recorded, resulting in high coral mortality on many reefs (Eakin et al., 2019; Bove et al., 2022; Cetina-Heredia and Allende-Arandia, 2023). Prior to 2023, the Cayman Islands had experienced seven thermal stress events exceeding 4 DHW, reaching 7.4 DHW in 2015 and 6.3 DHW in 2019 (NOAA Coral Reef Watch). However, none of these past thermal stress events exceeded the 8 DHW threshold where mass bleaching and mortality is expected to occur (Donner et al., 2005; Kayanne et al., 2017), emphasizing the severity of the 2023 thermal heatwave event. In the Spring of 2024 as the impacts of the El Niño event began to impact the Southern Hemisphere, the fourth Global Bleaching Event was announced and the forecast for future years suggests temperatures will continue to increase (Reimer et al., 2024). These continued increases will likely be devastating for reef corals, as locally based management strategies cannot mitigate the impacts from the global stressor of climate change (Bruno et al., 2018, 2019; Baumann et al., 2022; Johnson et al., 2022b, a; Doherty et al., 2025). Even the most thermally tolerant genotypes have critical temperature thresholds and survival limitations. Based on our survival models, the thermally tolerant genotypes in our nursery would eventually suffer bleaching induced mortality under prolonged thermal stress. Understanding what those limits are will be imperative for

management and restoration decisions that aim to preserve coral reefs in the face of continued global climate change.

Conclusion

This study reveals the physiological response of more than 400 colonies of *A. cervicornis* as they go through a major thermal stress event. Our study shows that host genotype has a significant impact on survival in the face of extreme weather, with a limited number of genotypes (O and OB) acting as outliers with the capacity to survive prolonged heating events. As the impacts of global bleaching events continue to increase, future studies should incorporate additional physiological and genomic comparisons among representative genotypes to better understand the mechanisms driving temperature tolerance and resilience to mitigate the impacts of future heatwaves on restoration success.

Data availability statement

The datasets generated and analyzed for this study can be found in the following Zenodo repository <https://zenodo.org/records/14392687>.

Author contributions

LL: Methodology, Writing – review & editing, Software, Writing – original draft, Investigation, Visualization, Formal analysis, Data curation. JJ: Investigation, Visualization, Writing – original draft, Formal analysis, Writing – review & editing, Methodology, Supervision, Data curation. GG: Conceptualization, Project administration, Validation, Writing – review & editing, Supervision, Funding acquisition, Investigation, Methodology, Formal analysis, Resources, Visualization, Data curation, Writing – original draft.

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Conflict of interest

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