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CENTRAL CARIBBEAN MARINE INSTITUTE

THE UNIVERSITY of NORTH CAROLINA at CHAPEL HILL

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INSIGHTS FROM ECOPHYSIOLOGY EXPERIMENTS AND SUGGESTIONS FOR IMPROVED CORAL RESTORATION

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BACKGROUND

Over the past several decades, Caribbean corals have undergone drastic declines (Contreras-Silva et al., 2020; Cramer et al., 2020), with Caribbean wide coral cover dropping to roughly 5-10% (Gardner et al., 2003). While losses are even more severe on heavily impacted regions such as the Florida Reef Tract, where coral cover is roughly 4% (Toth et al., 2019), remote and highly protected atolls are still at threat (Sanchez et al., 2019).

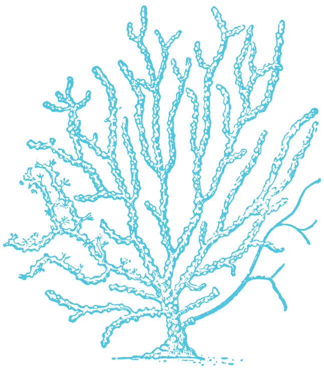
A myriad of environmental impacts are linked to these declines and include but are not limited to coastal development (DeGeorges et al., 2010; Ryan et al., 2008), novel diseases (Alvarez-Filip et al., 2019; Estrada-Saldivar et al., 2020; Hayes et al., 2020; Aronson & Precht 2001), and thermal stress events (Eakin et al., 2005; Munoz-Castillo et al., 2019). Persistence of chronic anthropogenic stressors and continued increases in their severity and frequency further constrain the recovery capacity of corals leading to bleak predictions for the future stability of coral reefs (Jones et al., 2022; Gonzalez-Barrios et al., 2020).

Among the first documented incidence of coral decline directly attributed to a specific cause was the regional die off of Acropora cervicornis and A. palmata in Caribbean and Gulf of Mexico in the early 1980s due to an outbreak of White Band Disease (Aronson and Precht 2001). Prior to the disease outbreak, Acropora spp. dominated shallow water reef zones, providing invaluable ecosystem services including shoreline protection through the disruption of wave action (Ghiasian, et al., 2020) as well as habitat for small and juvenile fishes that may have supported culturally valuable fisheries (Wilson et al., 2008). Within the first decade of the disease outbreak, however, the genus declined from >60% to <5% cover (Aronson & Precht 2001). This decline has only continued throughout the Caribbean, leading to both species being listed on the IUCN Endangered Species list.

The virtual absence of Acroporid corals at the shallow zones of most reefs today represents an unnatural state for modern Caribbean reef ecosystems and has profoundly altered the structure and functioning of Caribbean reef ecosystems. Thus, in the last decade significant effort has been allocated to restoring Caribbean coral reefs, primarily focusing on A. cervicornis and A. palmata due to their vulnerable status, historical ecological importance, and branching nature which allows them to grow 5 to 10 times faster than bouldering corals (Gladfelter et al., 1978; Lirman et al., 2014). Coral restoration, consisting of outplanting nursery-raised Acroporid corals to degraded reefs to rebuild reef structure and function, is an increasingly popular approach to confront local declines in coral abundance. Inspired by successful restoration strategies used to restore other habitats, contemporary coral restoration approaches primarily consist of outplanting nursery-raised corals to degraded reefs. Propagation and outplanting of nursery-grown corals has become so popular that coral restoration efforts are increasingly capable of augmenting coral populations at ecologically meaningful scales. Major progress in this industry has been made by several government and conservation-focused Non-Governmental Organizations (NGOs) in Southeast Florida and the Caribbean spearheaded by early efforts of the Coral Restoration Foundation, MOTE Marine Laboratory, and SECORE International.

Many of the initial techniques are still used, where corals of opportunity or fragments of wild adult corals are grown in either sea-based or land-based nurseries and periodically fragmented to create "new" individuals that populate the nursery. Early studies focused on providing optimal rearing conditions in these nursery environments, either in situ or ex situ, to maximize their growth as measured through Total Linear Extension (TLE; Johnson et al., 2011; Maneval et al. 2021). These efforts grew in popularity and thus in magnitude, becoming a large focus of conservation organizations. In Southeast Florida alone, thousands of A. cervicornis fragments have been grown in nursery settings and subsequently outplanted onto the reef, with one organization planting over 15,000 fragments of this species over a 5-year period. However, long-term monitoring of outplanted fragments shows highly variable results, even within one reef region, suggesting large-scale genetic and environmental variables may be important to consider when planning restoration work (van Woesik et al., 2020).

As new information is gathered about optimal growth conditions and maximum success rates, Acropora restoration and outplantating efforts continue to evolve. For example, several groups now incorporate aspects of sexual reproduction focused on cross-fertilizing gametes from parents with desired traits such as disease resilience or high thermal tolerance (Koch et al., 2022a,b), which has the capacity to upscale restoration on an industrial scale (Banazsack et al., 2023). These new advancements have been used as a part of developing Resilience Based Management strategies of corals, which aim to protect genetic diversity and maintain pathways for gene transfer through sexual reproduction (Mcleod et al., 2019). However, assisted evolution via selected cross-fertilization relies on information about adult colony stress-susceptibility (or rather stress-resilience) and reproductive capacity (Koch et al., 2022a,b). In Florida, recent work by Cunning et al. (2021) examined the thermal tolerance range of several corals across restoration sites along the Florida reef tract by measuring photosynthetic efficiency of nursery reared corals in response to a range of temperatures. Interestingly, they found that while differences in coral thermal tolerance existed among nursery sites, it was not related to historical Monthly Mean Maximum Temperature. Furthermore, a greater proportion of the variability of thermal tolerance occurred within nurseries, rather than between them, suggesting that genetic variability across individuals likely impacted thermal tolerance more strongly than past environmental conditions. Symbiont consortia can also impact thermal tolerances and thus a great deal of effort has also gone into Symbiodinacae species identification for nursery corals, as well as inoculation studies using thermally tolerant symbiont species (O'Donnel et al. 2019; Davies et al., 2023; Minjie et al., 2023). While increased temperature is a major threat to the success of restoration, so is disease susceptibility as outbreaks of White Bank Disease continue to affect Acropora spp. Thus, it is also important to identify adult colonies that are resilient to diseases that could be used in downstream sexual reproduction experiments (e.g. Koch et al. 2022).



These studies, along with investigations into potential tradeoffs with other desirable traits, have helped to inform the restoration choices of A. cervicornis in Florida. Combining several ideal factors such as thermal tolerance and disease resistance to produce resilient individuals that, once outplanted, will reproduce and pass on desired traits to the next generation (Humanes et al. 2021; Koch et al., 2022 a,b). Fate-tracking these "resilient" individuals allows scientists to provide data-driven advice to restoration practitioners that will increase the efficacy of restoration success and guide assisted evolution and trait selection. However, few studies follow outplanted corals for more than 12 months, and thus a major knowledge gap in the success of these efforts remains.

Figure 1.

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Figure 2a.

CCMI CORAL NURSERY

Initiating a science-based restoration program in the Cayman Islands in 2011, CCMI has been and will continue to be a pioneer in the coral reef restoration arena. The future of coral restoration efforts is dependent on our success, as ours is one of the few restoration projects that includes research-integrated solutions to better understand how restoration can contribute to the wild coral population and how we can unlock the secrets to coral resiliency for the future. Current restoration empirical investigations coupled with available long-term ecosystem data at CCMI provides the basis for furthering knowledge of reef resilience. Our previous work found that survival and growth were highest at our deeper nursery (15m) compared to our shallow nursery (5m) (Maneval et al. 2021). Moreover, monitoring of White Band Disease outbreaks and recovery in our nursery shown the benefits of maintaining genetically diverse assemblages within individual nursery frames (Brown et al. 2022). Regarding outplanting, we have found a 10-fold increase in survival by planting corals onto three-dimensional domes instead of directly onto the reef (CCMI 2020 annual report). Additionally, we found significantly higher survival and less disease when outplanting to 20m compared to 5m depth (CCMI 2021 annual report). To better quantify the potential for outplant success by individuals, CCMI recently conducted a thermal stress experiment along with subsequent outplanting and fate-tracking of A. cervicornis fragments on Little Cayman Island. Here we present this work along with recommendations to improve long term restoration success based on our results.

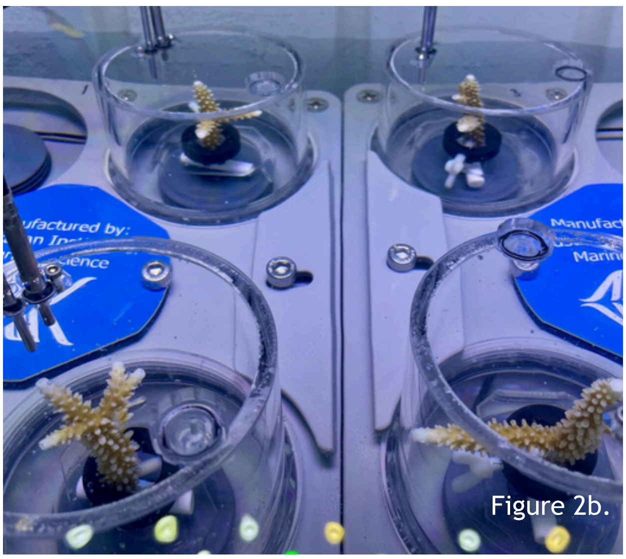


Figure 2b.

PROJECT METHODS

Fragments were collected from the nursery based on their previously identified categorical genet (Drury et al. 2017), sub-sampled for downstream molecular analysis, and brought to a land-based nursery and wet-lab for thermal tolerance analysis.

Thermal tolerance was assessed using Thermal Performance Curves (TPCs) where photosynthesis and respiration are used as a proxy for coral performance. Oxygen production and consumption were measured using a closed chamber system with real-time oxygen and temperature probes as in Silbiger et al. (2019) and Gould et al. (2021). To create the TPCs, a single fragment of an individual A. cervicornis genet was exposed to 8 temperatures ranging from 28C to 37C (28, 30, 32, 33, 34, 35, 36, 37^{0}C), under a ramp-up temperature scenario.

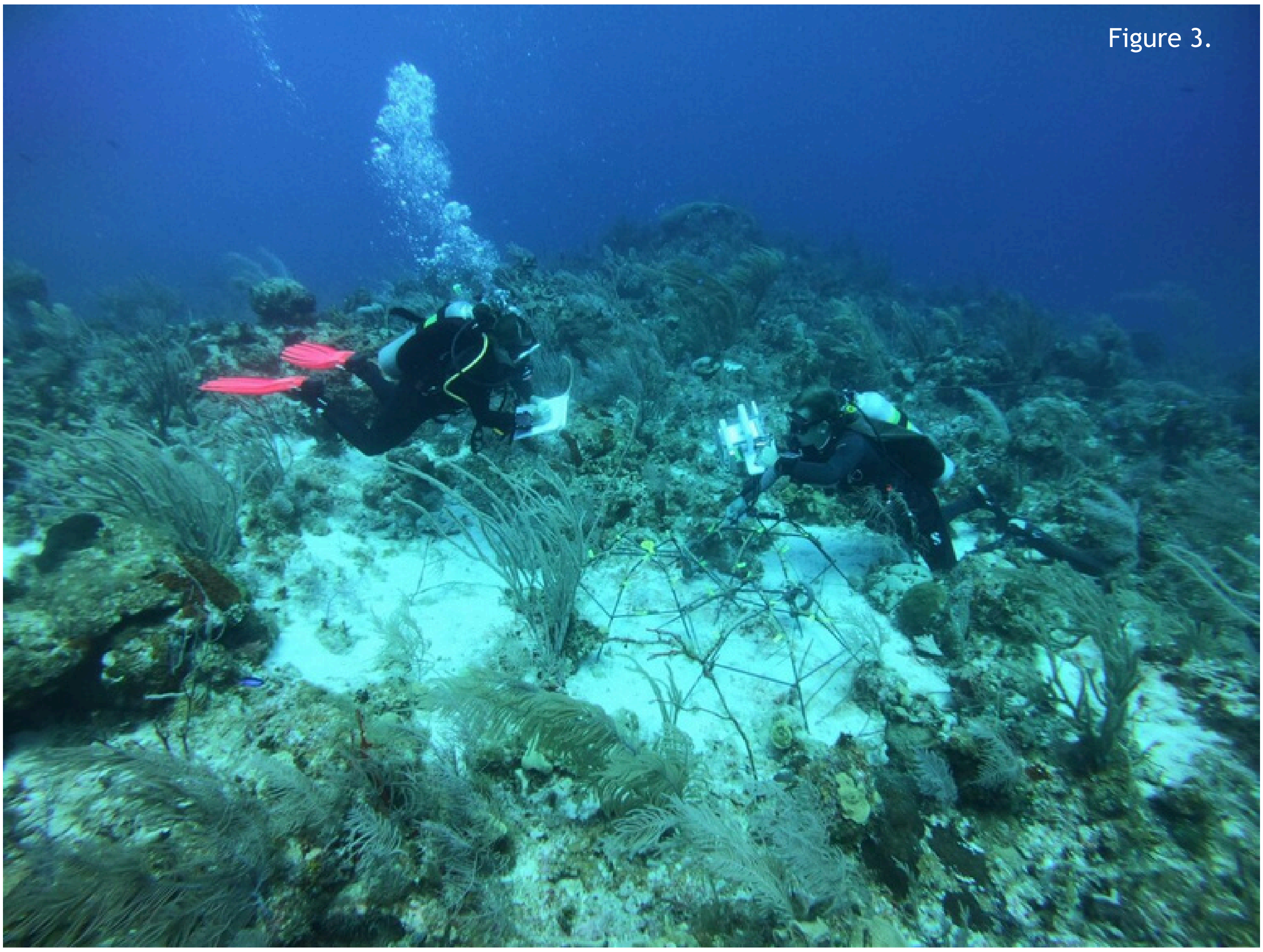
A total of 8 known genotypes from the nursery were tested, with 3 replicate individuals representing each genotype. Temperature in the chambers was controlled ($\pm 0.1^{0}$C) by a thermostat system (Apex Aquacontroller, Neptune Systems) using a chiller (AquaEuroUSA Max Chill-1/13 HP Chiller) and heaters (AccuTherm Heater 300W). Oxygen concentration was measured in each chamber every second for 15 minutes under saturating light conditions, after which the system was covered, and measurements continued for another 30 minutes in absolute darkness. Light levels were based on initial P/I curve to determine the PAR which induced the optimal photosynthetic rate at ambient temperature. The absolute values of net photosynthesis plus dark respiration produced gross photosynthesis (GP). Two blank control chambers (FSW and magnetic stir-bar only) accounted for the oxygen production and consumption from micro-organisms within the seawater. This background metabolic activity was subtracted from each corresponding experimental chamber. The rates of oxygen flux were additionally corrected for chamber volume and surface area of the fragment using the paraffin wax dipping method (Stimson and Kinzie 1991; Holmes et al.,2008). Bayesian hierarchical models with Markov Chain Monte Carlo (MCMC) simulations were then used to estimate coral thermal tolerance metrics for GP (Silbiger et al. 2019; Gould et al. 2021). Thermal performance parameters across selected genotypes were extracted with the RTPC package and NLS multi-start using a Sharpe-Schoolfield model and bootstrapping and included: maximum critical temperature (CTmax), activation energy (e), deactivation energy (eh), thermal safety margin, and optimal temperature (Topt).

Replicate ramets of genet were then outplanted in a common garden scenario on a series of dome structures (n=3) serving to creating three-dimensional structure as well as lifting outplants off the sediment to reduce the chances of disease transmission. A total of 3 replicates of each of the 8 genotypes were outplanted onto each structure for a total of 9 replicates per genotype. Outplants were subsequently assessed for health status (healthy, pale, bleached, disease, predation, dead, missing) after 11 and 16 months (April 2023 and September 2023, respectively). In addition, at each time point Total Linear Extensions (TLE) was also measured to estimate growth rates.

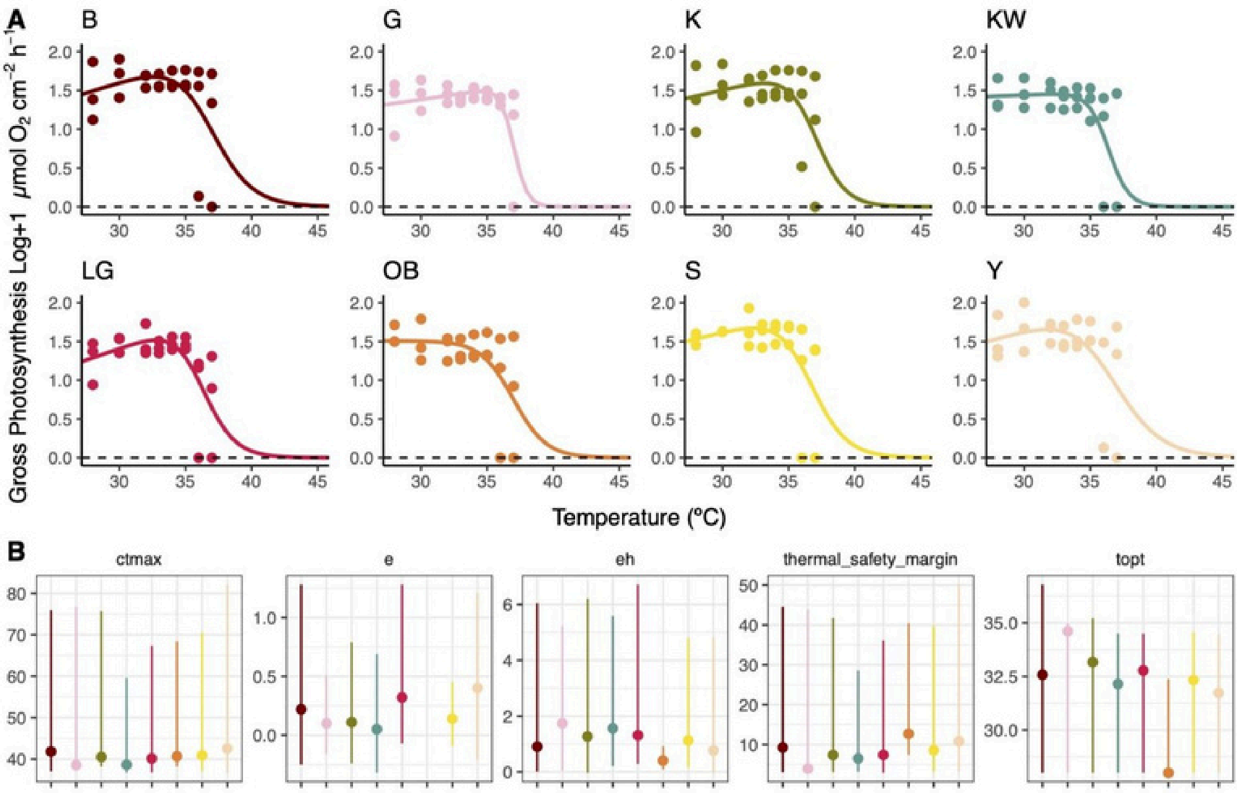
RESULTS & DISCUSSION

Overall, our thermal performance results for temperature tolerance were similar among genotypes, however, a few key performance parameters stood out. For example, genotype OB had the lowest deactivation energy and the most gradual slope post thermal optima as well as the highest thermal safety margin, suggesting that this genotype may have the least severe bleaching response. In contrast, genotype G had the highest deactivation energy and the steepest slope, indicating a severe bleaching response would be expected (Figure 3). However, a clear “winner” or “loser” cannot be identified, and thus these data alone would suggest a bet hedging approach that maintains maximum genetic diversity is likely to be the best method for restoration practitioners.

Figure 3.



Over time, we found continued losses of our outplanted corals, regardless of genotype, with survival probability dropping below 50% after the 11-month period (Figure 4). The summer of 2023 was the warmest on record, with Little Cayman Island experiencing a record 19.5 degree heating weeks (NOAA). This provided an opportunity to monitor the response of the common garden outplants to a natural bleaching event and compare to laboratory-based assessments of bleaching tolerance. At the end of the bleaching event, most corals were either severely bleached or dead, and only genotype (KW) had any remaining healthy colonies (Figure 5).



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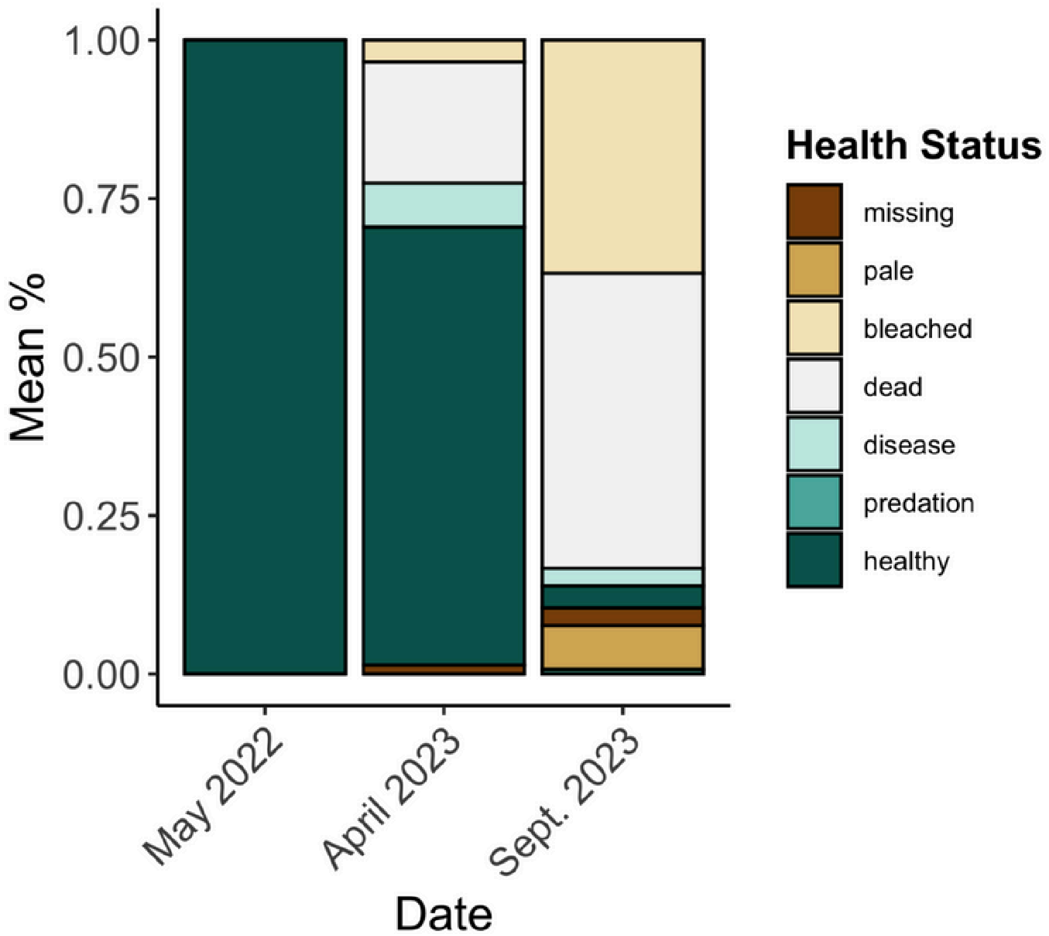

Figure 5a.

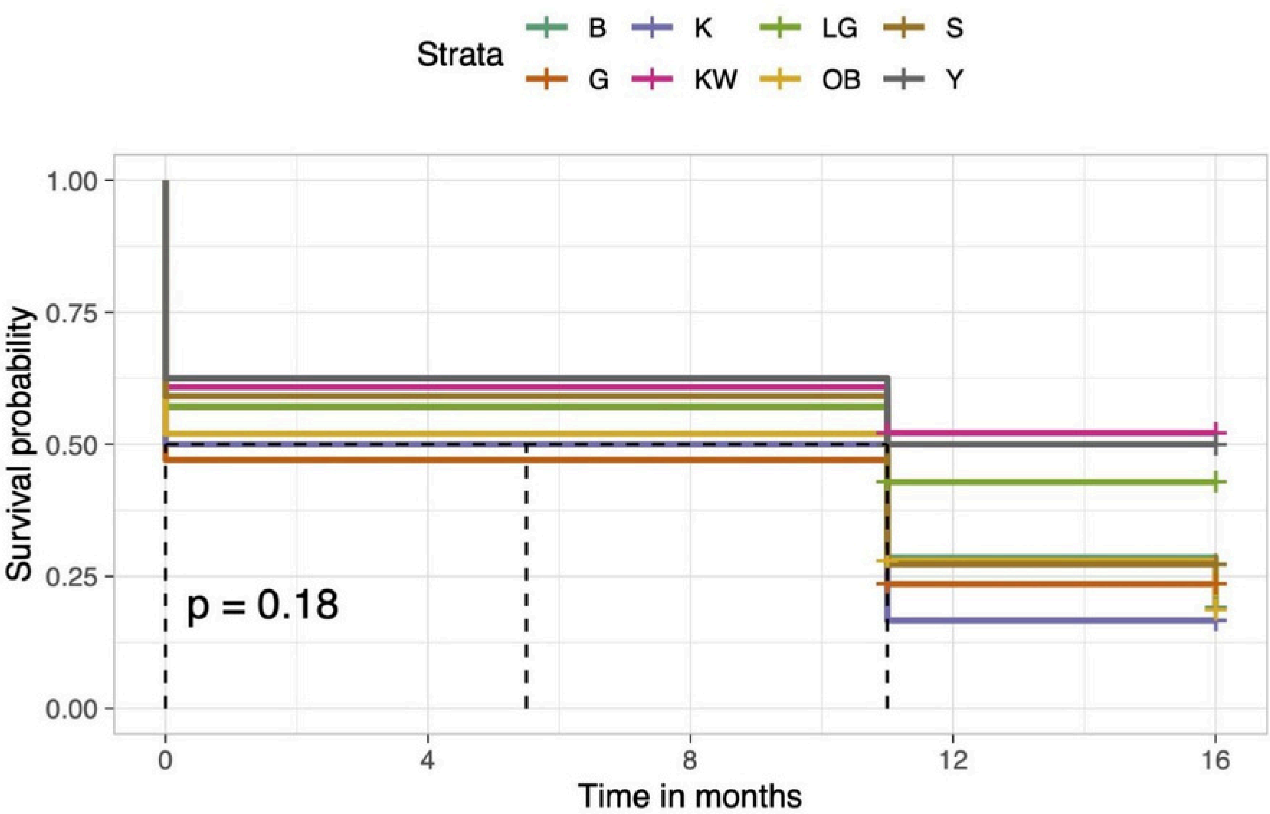

Figure 5b.

Our fate-tracking data showed no significant differences in growth rates or bleaching frequency based on genotype, however, certain genotypes appeared to fair better over time than others. For example, genotypes KW and LG had the lowest growth rates compared to all other genotypes, while OB, K, and KW showed the lowest percent bleaching response (Figure 6). While no significant correlations were found, our thermal performance data suggested that genotype OB would show a less severe bleaching response, which corresponded with our fate-tracking results. Thus, with increased replication, thermal performance curves may be a valuable tool in examining realized thermal resilience. In addition to bleaching and growth, disease status was recorded on all outplants across sampling points. Outcomes of these data suggest that the most thermally tolerant genotypes tend to have lower growth rates and higher disease susceptibility, suggesting a tradeoff between growth, disease resistance, and bleaching tolerance. Findings of biological tradeoffs between desirable traits in restoration corals are not unique to this study (Cornwell et al., 2021; Ladd et al., 2017; Quigley et al., 2021), although it is not universal among desirable traits (Koch et al., 2022a,b). Yet, potential tradeoffs among desirable traits provides further evidence for the value of increased genetic diversity in nursery corals.

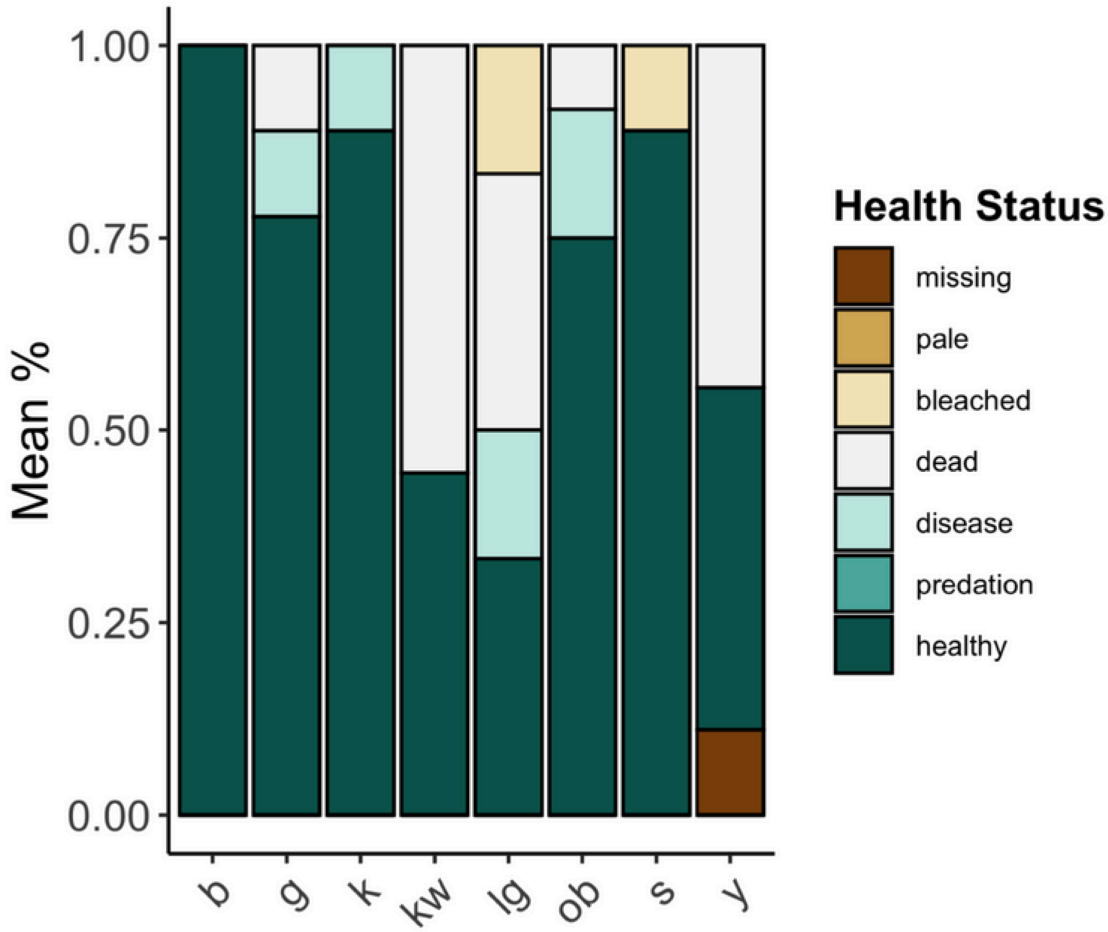

Figure 6a.

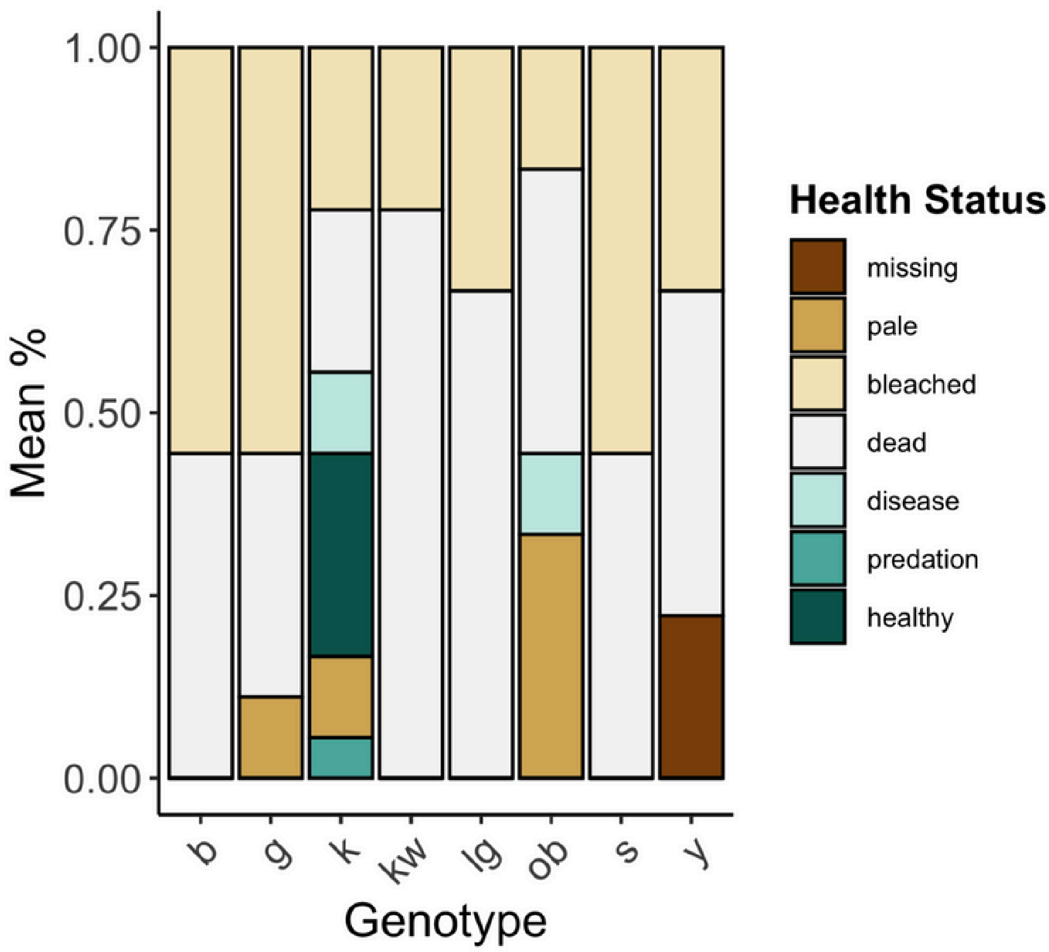

Figure 6b.

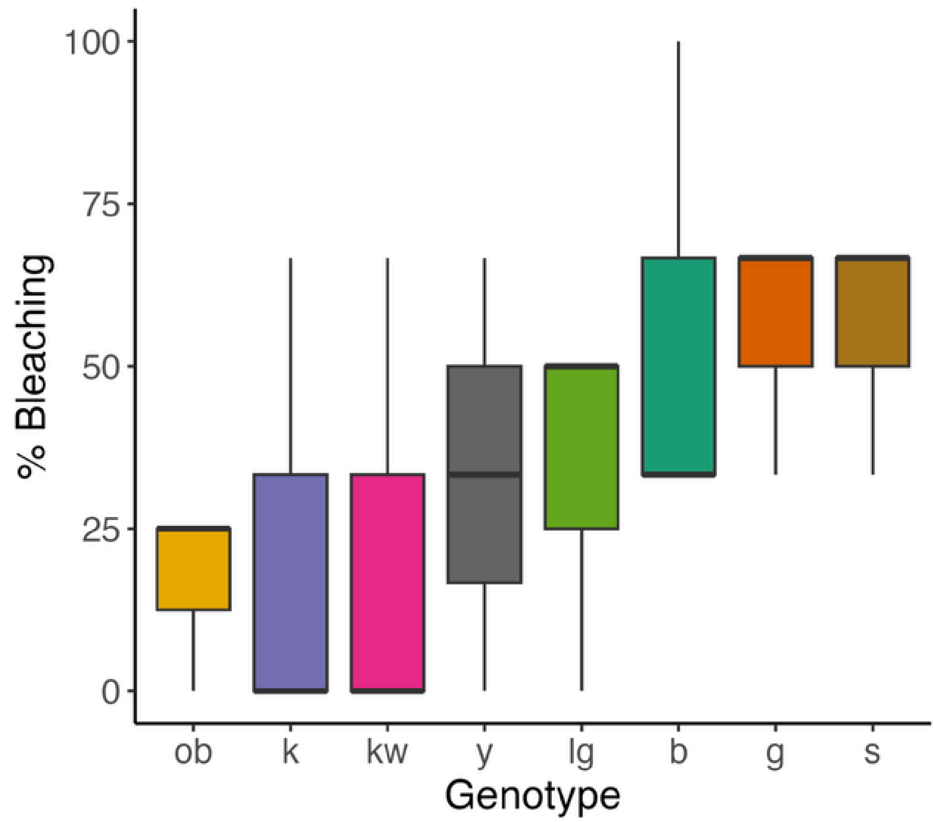

Figure 7a.

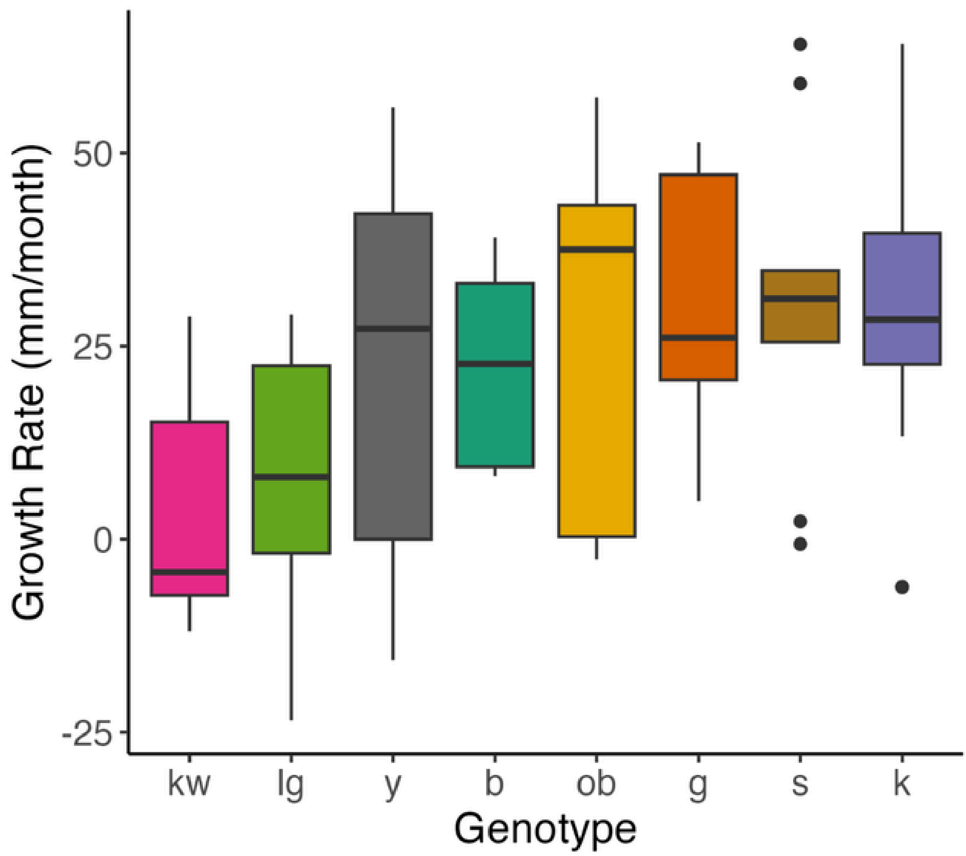

Figure 7b.

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RECOMMENDATIONS

The data from this study shows that there is unlikely to be one individual or genet of A. cervicornis which is resilient to a broad range of stressors that could be considered a super coral. While some colonies had stronger tolerance of acute thermal stress, these were not necessarily the genets that were likely to grow fastest, withstand disease most effectively, or tolerate long term thermal stress exceeding 19 Degree Heating Weeks. These kinds of tradeoffs in coral stress-tolerance are well documented across the field and suggest that maintaining maximum biological diversity in nursery settings may be the best and only way forward in reef restoration. This genetic diversity could be important to capture in both sexual and asexual outplantation efforts. Whether facilities aim to utilize asexually reproduced adult-coral outplanting, or sexually reproduced larvae, it will be vital to maintain maximum biological and genetic diversity rather than selecting hardy or resilient individuals. This management practice will avoid artificially imposed genetic bottlenecking in favor of the largest genetic “toolbox” a coral population can have, giving outplants the highest likelihood of population-level success.

The widescale bleaching in 2023 that affected the Caribbean and Floridian reefs also provides reef practitioners with the chance to re-assess restoration protocols as we move forward, with many sites having to restart nurseries from near scratch. We recommend that at this time, nurseries be stocked with the widest genetic diversity of adult colonies possible for future endeavors. This season has taught us that biological tradeoffs may not only be a downfall of selective breeding but could be utilized as the greatest asset in the future of coral restoration practices.

Considering the overall Caribbean coral decline beyond Apropora spp., it has become more important than ever to diversify not only the genetic bank of each species but also the species themselves, incorporating corals of varied growth forms. While Acroporids are historically valuable in the Caribbean, even with the breadth of genotypes remaining, the genus may not possess the ability to cope with extreme heat events that are highly likely to continue at rates of increased frequency and severity. To restore reefs to their historical biological complexity, or even to maintain what remains, restoration practitioners need to broaden the species included to a wider variety, including those vulnerable to new diseases.

Incorporating more slow-growing and structure-forming hermatypic corals will also increase our capacity to maintain reef rugosity, accretion rates, and biological diversity in a longer-lasting way. In addition, incorporating weedy species into these practices may provide longer survivorship of outplants, allowing reefs to persist even through challenging environmental conditions.

Ultimately, it has become exceedingly clear that to restore Caribbean reefs or even to maintain them using supplemental coral outplantation, we must consider modern technologies as a requisite part of the toolbox. Utilising molecular sequencing technologies, which are gradually becoming more accessible, may be vital to understanding the genetic lineage and connectedness of coral populations, protecting against genetic bottlenecking within any one restoration species. Likewise, our results suggest that thermal-performance assessments may be valuable in determining individuals with the highest temperature tolerances. Restoration through sexual reproduction will also allow for more highly scalable practices as well as increasing genetic diversity through the potential for genetic recombination.

Combining these tools will give reef practitioners the greatest chance at making lasting and impactful change. Continued focus on coral symbiont populations and related environmental stressors could lay a pathway for using symbiont inoculation in or population management in nursery corals and larvae. Lastly, increasing the species richness of both sexual and asexual restoration practices will create the opportunity for a more wholly restored reef ecosystem. In following with consensus across the field (Banaszak et al., 2023; Hughes et al., 2023; Johnson et al., 2011; Mcleod et al., 2019), it is these adaptations of strategy that will help to propel meaningful coral reef restoration practices further into the 21st century.

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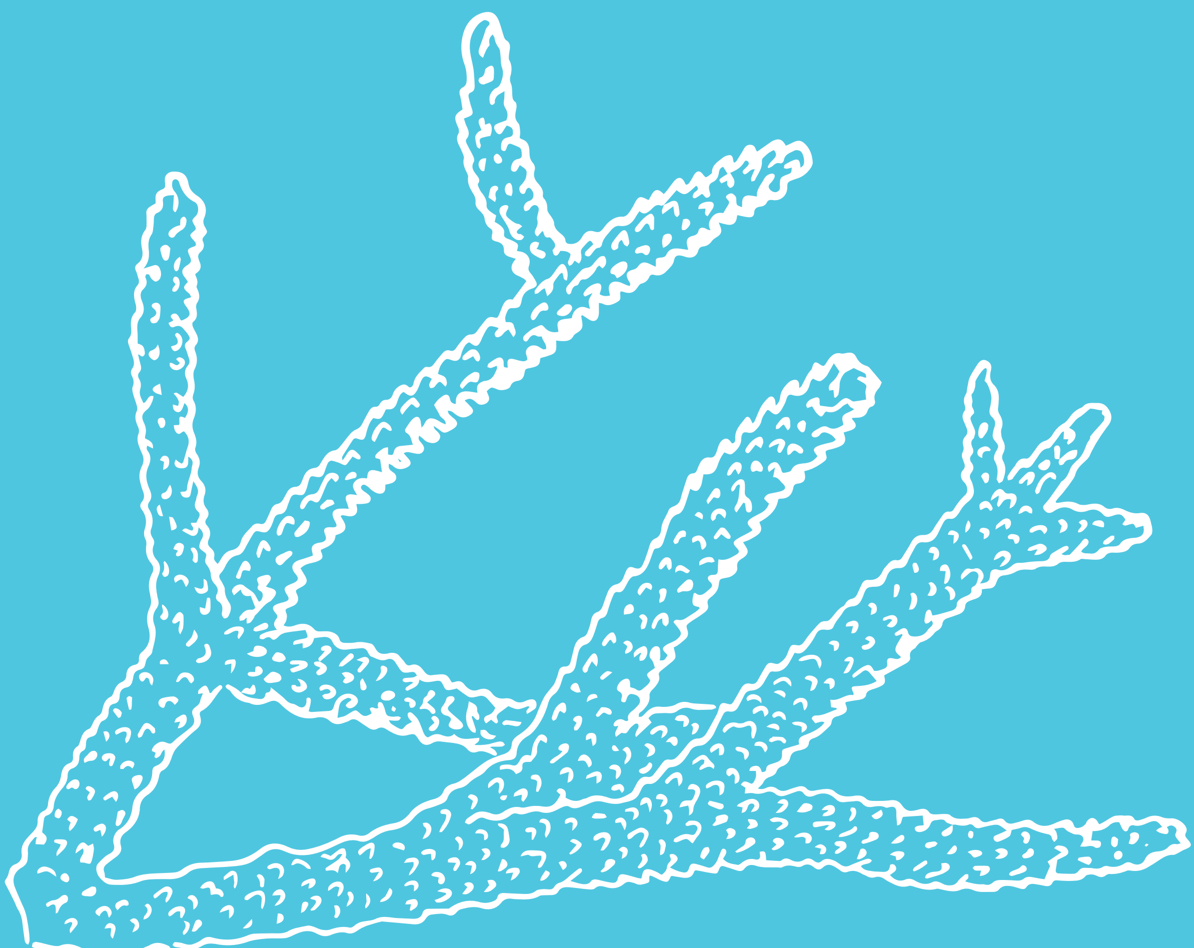

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FIGURE LEGENDS

Figure. 1. Image of Acropora cervicornis colonies growing in the CCMI coral nursery at approximately 15m depths in Little Cayman.

Figure. 2. (a) Image of lead researchers G. Goodbody-Gringley and J. Bruno with the thermal performance experimental set up. (b) Image of incubation chambers held in a water bath at constant temperature, affixed with oxygen and temperature probes, each containing an individual A. cervicornis fragment.

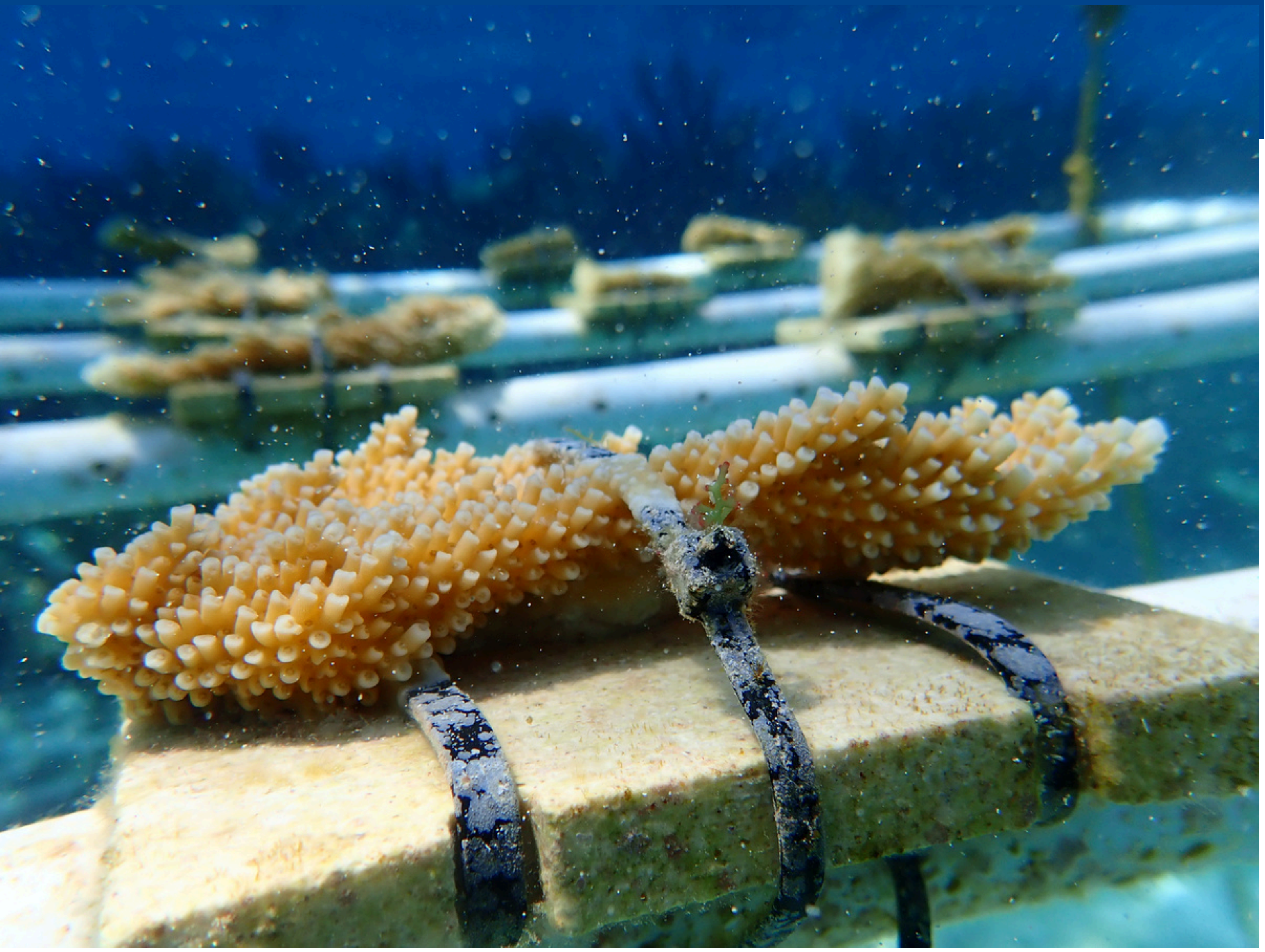
Figure. 3. Image of divers conducting health assessments on a common garden outplant site. Each site contained an equal number of replicate fragments representing each of 8 genotypes that were haphazardly placed on the dome.

Figure. 4. Results of the thermal performance experiments.

Figure. 5. (a) Health state of all outplanted corals after initial outplanting in May 2022, secondary assessments in April 2023, and final assessment in September 2023. (b) Kaplan-Meier survival probability curves by genotype.

Figure 6. Health state by genotype in (a) April 2023 and (b) September 2023.

Figure 7. (a) Bleaching prevalence and (b) growth (total linear extension) by genotype at the end of the fate-tracking in September 2023.



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