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NOTE

Thermal history influences lesion recovery of the threatened Caribbean staghorn coral *Acropora cervicornis* under heat stress

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Abstract Anthropogenic climate change is the biggest threat to coral reefs, but reef restoration efforts are buying time for these ecosystems. Lesion recovery, which can be a determinant of colony survival, is particularly important for restored species. Here, we evaluate lesion recovery of 18 genets of *Acropora cervicornis* from Florida reefs with different thermal regimes in a temperature challenge experiment. Genets demonstrated significant variability in healing, which greatly slowed under heat stress. Only 35% of fragments healed at 31.5 °C compared to 99% at 28 °C. Donor reef thermal regime significantly influenced lesion recovery under heat stress with corals from warmer reefs demonstrating greater healing than corals from cooler reefs, but did not influence recovery under ambient conditions. These findings should encourage practitioners to utilize rapidly healing genets, avoid fragmentation in high temperatures, and incorporate assisted relocation by moving corals from warmer to cooler reefs, where they might succeed under future climate conditions.

Keywords *Acropora* · Coral restoration · Local adaptation · Lesion recovery · Thermal tolerance

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Introduction

Coral reef ecosystems are experiencing unprecedented declines caused by interacting stressors that include pollution, overfishing, diseases, and anthropogenic climate change (Harborne et al. 2016). At global scales, high seawater temperatures have led to increases in the extent, frequency, and duration of coral bleaching events that have affected even the most protected reefs (Eakin et al. 2019). The Caribbean acroporids have undergone severe population declines of 80–90% since the 1970s or earlier, due to human pressures and a severe disease outbreak (Aronson and Precht 2001; Cramer et al. 2020). With limited population recovery, active coral propagation and reef restoration have become common tools used to help restore these taxa, particularly staghorn coral (*Acropora cervicornis*), and their associated ecosystem services (Young et al. 2012).

As many restoration programs focus on the asexual propagation of branching corals, it is important to identify individuals with favorable traits that can be selectively propagated to maximize success and enhance the climate resilience of restored coral populations (Lirman and Schopmeyer 2016; National Academies of Sciences, Engineering, and Medicine 2018). Phenotypic traits proposed by Baums et al. (2019) to evaluate genotype performance include: (1) partial mortality; (2) lesion healing;

(3) growth rates; (4) bleaching and disease resistance; and (5) sexual reproduction. Life-history attributes such as mortality and growth (Lirman et al. 2014), disease resistance (Miller et al. 2019), bleaching resistance (Lohr and Patterson 2017), and fecundity (Vargas-Angel et al. 2006) have been well studied for staghorn coral. While examined in congener *Acropora palmata* (Bak 1983; Meesters and Bak 1995; Lirman 2000*),* to date, patterns and drivers of lesion recovery, including variation by genotype, have not been evaluated for *A.cervicornis,* representing a research gap that is addressed in our study.

Wound healing is of particular interest because lesions are created throughout the coral gardening process and during frequent natural fragmentation events. Healing reduces the likelihood of colonization by algae, borers, and pathogens that can cause mortality (Highsmith 1982). Thus, identifying genotypes with greater recovery potential that can be outplanted at locations where corals are more prone to fragmentation, such as areas with high wave energy, is a pressing restoration need. Also, since thermal stress can slow or suspend lesion recovery (Meesters and Bak 1993; Bonesso et al. 2017), it is important to evaluate the effect of high temperature on lesion repair to understand how performance might vary seasonally or under ocean warming scenarios.

Novel interventions, such as managed relocation and assisted gene flow, are currently being explored to enhance the climate resilience of reef restoration efforts (National Academies of Sciences, Engineering, and Medicine 2018). Managed relocation requires that phenotypes of interest depend on fixed (genetic) effects that will allow these corals to maintain attributes after relocation. Some coral traits, such as thermal tolerance, are commonly associated with symbiont identity (Silverstein et al. 2017), but staghorn in Florida typically only host *Symbiodinium fitti* (Lirman et al. 2014). Consequentially, variation in the performance of this species in Florida is usually attributed to acclimatization or adaptation of the coral host. Previous research has found that colonies collected from different reef environments maintain differences in growth (Lirman et al. 2014) and disease resistance (Miller et al. 2019) after relocation to common garden conditions. Here, we used a temperature challenge experiment to evaluate patterns of lesion recovery among staghorn genets that were originally collected from a wide range of environments across the Florida Reef Tract that vary in their thermal regime. We hypothesized that colonies from warmer environments would be able to heal lesions more rapidly under heat stress. Such findings would support the movement of genotypes from warmer reefs to cooler restoration sites that are expected to warm with anticipated climate change.

Materials and methods

We collected 18 staghorn genets from reefs spanning > 100 km of the Florida Reef Tract and cultivated them under common-garden conditions in an in-water coral nursery off Key Biscayne, Miami, Florida, USA (25.676° N, 80.098° W; depth = 9 m, Fig. 1) for 2–6 years. Colonies were collected from distances exceeding the 500 km threshold used to ensure distinct genets (Vollmer and Palumbi 2007). Within reefs, colonies were collected with a minimum separation of 5 m, exceeding the distance documented by Drury et al. (2016) for distinct genets within close aggregations. We then assessed lesion healing rates under control and elevated-temperature conditions in a laboratory experiment. Ten 5-gallon aquaria equipped with pumps and air bubblers were used as experimental units and were allocated between two large tanks (2 × 0.75 × 0.25 m). Heaters placed within one of the large tanks were used to reach the desired high temperature for treatment corals. Replicate fragments of each genet were collected from the coral nursery, mounted onto acrylic pucks, and allowed to acclimate for two weeks at ambient temperatures in the laboratory. Fragments ($N = 5$ per genet per treatment) contained an apical polyp and were 2.66 ± 0.40 cm and 2.82 ± 0.31 cm (mean ± SD) in total linear extension (TLE) for control and heated corals, respectively. These fragments were randomly assigned to the aquaria with each genet present in each of the 10 aquaria, and fragment and aquaria positions were rotated every other day. Water changes were made every day using filtered seawater pre-heated to the desired temperature. Corals were fed every other day with Reef Chili.

Skeletal lesions were created by removing fragment tips with a band saw. Lesion areas were 0.35 ± 0.19 cm^2 and 0.32 ± 0.15 cm^2 (mean ± SD) for control and heated corals, respectively. The following day, the temperature of the exposure tank was raised daily by 0.5 °C increments, from 28 °C to 31.5 °C over 7 days, and then maintained at 31.5 °C (32.03 ± 0.48 °C (mean ± SD)). The ambient tank remained at 28.02 ± 0.27 °C (mean ± SD) throughout the experiment. Corals were surveyed every other day following lesion generation, and the amount of lesion healed was classified visually in 25% increments, from 0 to 100% healed (Fig. 2). To avoid excessive mortality, the experiment was terminated when no additional fragments within the warm tank were observed to heal for one week.

Pearson Chi-square tests were used to test for independence of the frequency of colonies healed by temperature treatment. To evaluate the role of thermal history in performance under temperature stress, we divided the genets into two groups based on the maximum monthly mean temperatures (MMMs) of the source reefs. MMM

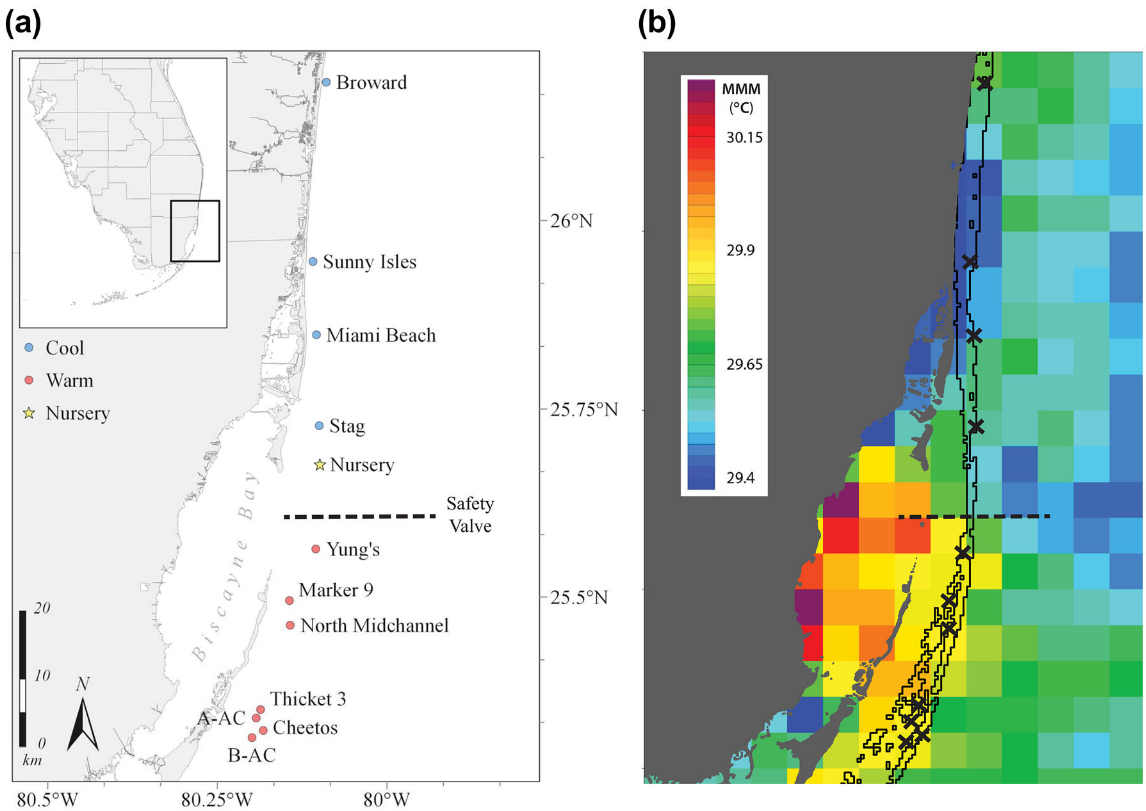

Fig. 1 **a** Key Biscayne Nursery and donor reef locations. Circle colors correspond to donor reef 4-km resolution maximum monthly mean (MMM) sea surface temperature data in which red indicates an MMM ≥ 29.92 °C and blue indicates an MMM < 29.92 °C. **b** MMM sea surface temperatures derived from harmonic analysis of the advanced very high-resolution radiometer (AVHRR) Pathfinder version 5.0 from 1982 to 2008. The Florida Reef Tract is outlined in black, and donor reef locations are indicated by black X's. The dashed horizontal line indicates the geographic location of the temperature grouping threshold, which is also the location of the "Safety Valve" tidal flow channels

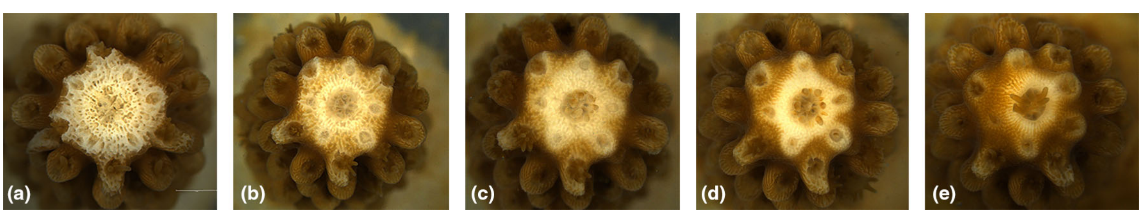

Fig. 2 Incremental lesion healing scoring system including **a** 0% healed; **b** 25% healed; **c** 50% healed; **d** 75% healed; and **e** 100% healed fragments

data were determined from 4-km resolution monthly sea surface temperature climatology derived from harmonic analysis of the advanced very high-resolution radiometer (AVHRR) Pathfinder version 5.0 temperature time series data for 1982–2008 (Casey et al. 2010). Genets from reefs with MMMs ≥ 29.92 °C, the median MMM of the dataset considering all fragments, were classified as from "warm" environments (10 genets), and those from reefs with lower MMMs were classified as from "cool" environments (8 genets). 29.92 °C also represents the MMM at the southern end of the "Safety Valve," series of tidal flow channels between the Ragged Keys and Key Biscayne, north of which all "cool" genets are located and south of which all the "warm" genets are located (Fig. 1). While corals were collected outside the period used to calculate historical temperature patterns (2014–2018), it is expected that the temporal offset (maximum of 10 years) would not have resulted in a significant change in regional climatology of temperature patterns. We constructed a Cox proportional hazards model using the package "survival" in R version 1.3.959, with temperature treatment (ambient vs. heated) and donor reef grouping (warm vs. cool) as fixed effects, and the response event being complete lesion recovery. We stratified the model by temperature treatment because this covariate violated the proportional hazards function assumption, and we included an interaction between temperature treatment and thermal history group because this interaction significantly improved the model ($\chi^2_{1,163} = 25.1, p < 0.05$). Because of this stratification and interaction, we determined model coefficients for treatment groups separately (Kleinbaum and Klein 2012). To compare genet performance between temperature treatments, we examined the quantile rank of each genet within treatment groups based on proportion of colonies healed 12 days after wounding. We also conducted a Kendall rank correlation test between genet proportions healed under ambient temperatures versus under heat stress.

Results and discussion

Our laboratory experiment showed that thermal stress has a strong negative influence on the recovery of skeletal lesions in *A.cervicornis*. By the end of the experiment (24 days), 64% more fragments had healed under ambient temperatures than under heat stress ($\chi^2_{1,164} = 74.66$, $p < 0.001$). While colonies exposed to the heat treatment were observed to pale, none of the fragments fully bleached, and colonies within the control group did not show signs of color loss. Our findings agree with those of Meesters and Bak (1993) who showed that corals suspend lesion recovery under bleaching conditions.

Lesion healing rate varied significantly among genets under ambient conditions ($F_{17,81} = 2.66, p < 0.01$), but not among genets under heat stress because many fragments failed to heal. The proportion of colonies healed by genet after 14 days ranged from 0 to 100% under ambient temperatures and 0–60% under heat stress. We did not observe a significant correlation in performance by genet between proportion of colonies healed under control and warm conditions, indicating a lack of clear winners (genets that heal fast under any condition) and losers (genets that consistently heal slowly) ($T_{16,18} = 0.47$). Nevertheless, some genets did well in both treatments (North Midchannel-B, B-AC, and Marker 9), while a couple of genets did poorly in both treatments (Stagreef-B and Yung's-B.), suggesting that practitioners should evaluate genotypes within multiple environments (and not only within single coral nurseries) to select individuals for restoration purposes (Online Resource 1).

In addition, we document for the first time that donor reef thermal history plays a role in efficient lesion recovery under heat stress and provide evidence for thermal adaptation. There was a significant interaction between temperature treatment and thermal history in the stratified Cox model ($\beta = 0.52$, $Z_{1,164} = 2.18$, $p < 0.05$). Corals from warmer donor reefs demonstrated significantly greater healing than corals from cooler reefs under heat stress, with a 1.74 times greater Cox proportional hazard rate where the hazard event is healing ($\beta = 0.55$, $Z_{1,81} = 1.89$, $p = 0.05$), while there was no apparent effect of thermal history under ambient conditions (Fig. 3, Online Resource 2). Increased thermal tolerance of individuals from warmer and variable reef environments has been documented in other coral species and regions. Morikawa and Palumbi (2019) found colonies collected from warmer environments maintained heat tolerance after 8 months in a common garden in American Samoa. Kenkel et al. (2013) found colonies that were collected from an inshore reef exposed to temperature extremes in the Florida Keys maintained thermal tolerance in a laboratory experiment with no common-garden phase and linked these differences to significant genetic divergence.

Our results suggest that sourcing colonies from warmer reefs and outplanting them into cooler environments that may experience temperature increases in the future would enhance lesion recovery under heat stress and could be incorporated into strategies to increase climate resilience. We also recommend avoiding fragmentation when seawater temperatures near the species' bleaching threshold. However, when fragmenting under stressful thermal conditions, practitioners can increase the likelihood of lesion recovery by selecting genotypes sourced from warmer environments. Lastly, we recommend that restoration practitioners identify rapid healers through lesion recovery tracking and outplant these genotypes in higher abundance at restoration sites where colonies are more vulnerable to fragmentation. However, tradeoffs between regeneration and other valuable traits such as disease resistance need to be identified and taken into consideration when selecting for this particular phenotype. Due to the importance of lesion recovery for colony survivorship, particularly in

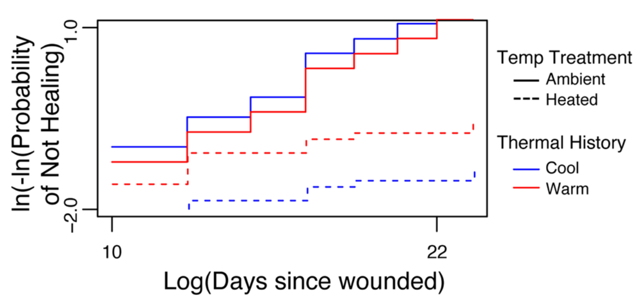

Fig. 3 Log(−log(survival)) curves as a function of time (log scale) using separate Cox proportional hazard models for the ambient temperature treatment (solid lines) and the warm temperature treatment (dashed lines), with thermal history (red indicating being from a warm reef and blue being from a cool reef) as a fixed effect. In this experiment, survival is analogous to not healing, the censored outcome. Negative log-log values indicate a higher survival probability or higher probability of not healing, while higher log–log values indicate a greater probability of healing

species that are routinely pruned for restoration such as *A.cervicornis*, we recommend that practitioners prioritize examining and exploiting this phenotype within their restoration programs.

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Compliance with ethical standards

Conflict of interest On behalf of all authors, the corresponding author states that there is no conflict of interest.

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