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Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*

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ABSTRACT: Coral restoration is gaining attention as a viable strategy to restore degraded reefs, with large-scale restoration efforts underway worldwide. However, our understanding of the drivers of restoration success lags behind restoration activities, generating significant knowledge gaps that may impede our ability to successfully restore coral reef communities. Here, we conducted a 21 mo field experiment to examine the influence of genotypic identity and diversity on coral growth, habitat production, and survivorship in restored corals. We used nursery-raised colonies of *Acropora cervicornis*, the predominant coral used for restoration in the Caribbean, to establish populations of either 1, 2, 4, or 6 distinct genotypes. Midway through our experiment, our study site experienced a 17 wk thermal stress event that allowed us to examine the influence of genotypic identity and diversity on the ability of restored corals to cope with thermal stress. After 21 mo we found no effect of genotypic diversity on restored corals, but that genotypes differed 3-fold in survivorship and 20 to 327% in habitat production. Initial growth rates showed a significant positive relationship with live tissue loss at the end of the experiment, suggesting a tradeoff between growth and the ability to recover from thermal stress. Our study suggests that genotypic identity is a critical factor to incorporate into coral restoration planning. Investigating the role of genotypic identity and diversity on the ability of restored corals to resist pervasive coral reef stressors, such as disease, predator outbreaks, and nutrient pollution, are critical steps in advancing coral restoration efforts.

KEY WORDS: Coral restoration · *Acropora cervicornis* · Genotypic diversity · Coral traits · Ecological restoration · Genetic diversity · Tradeoffs · Coral

INTRODUCTION

Coral reefs comprise the ecological, economic, and social backbone of tropical coastal communities worldwide (Burke et al. 2011). However, coral reefs are being lost at an alarming rate (Bruno & Selig 2007), particularly in the Caribbean where reefs have lost ca. 80% of their corals since the 1980s (Gardner et al. 2003, Jackson et al. 2014). To confront declines in coral cover, coral restoration (the process of outplanting nursery-raised corals to degraded reef sites) has become increasingly popular over the past decade (Young et al. 2012). However, coral restoration is time-consuming, costly, and in some cases, restored corals meet the same fate as the coral predecessors they were intended to replace. Accordingly, research identifying the mechanisms that dictate restoration success or optimize restoration strategies is sorely needed. To date, studies have investigated the influence of a variety of factors on the growth and survival of restored corals including outplant size (Garrison & Ward 2008), density (Ladd et al. 2016), genotype (Lirman et al. 2014), source location (Forrester et al. 2013), and species diversity (Cabaitan et

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al. 2015). However, despite recent progress, significant knowledge gaps in our understanding of coral restoration remain that may impede our ability to successfully restore coral reef communities.

One important gap is our lack of understanding how the genotypic diversity and identity of corals used for restoration affect the outcome of restoration efforts. Genotypic diversity can impact ecosystem function via complementarity among genotypes in ecologically important traits, such as biomass production or disease resistance (Fargione et al. 2007, Hughes & Stachowicz 2011). Alternatively, one or several genotypes can outperform others in a particular trait and drive population level patterns (i.e. the sampling effect; Loreau & Hector 2001). For example, Reusch et al. (2005) documented 4-fold differences in shoot density between restored seagrass *Zostera marina* genotypes when confronted with thermal stress. Indeed, *Z. marina* displays genotype-specific differences across ecologically important traits such as shoot biomass, production, and nutrient uptake (Hughes et al. 2009). Accordingly, genotypically diverse populations can better resist or recover from disease (Mundt 2002), species invasions (Crutsinger et al. 2008), herbivory (Peacock & Hunter 2001, Hughes & Stachowicz 2004), and environmental extremes (Reusch et al. 2005). Given the multitude of stressors influencing marine systems, environmental and biological context will likely influence intraspecific differences in important ecological traits. Thus, the differences in traits among genotypes may be an important driver of the impact of genotypic diversity in determining population performance. In the context of ecological restoration, genotype-specific traits may be especially important for choosing individuals that perform best or are robust to changes in environmental conditions in order to maximize restoration success.

However, on coral reefs, relatively little is known about genotype-specific performance of corals used for restoration, particularly when confronted with common stressors. This knowledge gap may hinder our ability to develop successful and sustainable coral reef restoration strategies (Baums 2008). Here, we address this gap by investigating the influence of genotypic identity and diversity on the growth and survivorship (henceforth referred to as 'performance') of restored corals. We assessed the success of restored corals based on survivorship and total linear extension of the coral skeleton, a proxy for the amount of habitat generated by an individual coral. This definition of success is based on a series of positive feedbacks that high coral cover and habitat complexity are posited to promote on coral reefs (Mumby & Steneck 2008).

Originally, we set out to test 2 main questions: (1) Does genotypic diversity of restored corals influence the success of coral restoration efforts? and (2) Do genotypes of restored corals vary in growth rates and habitat production? However, 2014 was the warmest summer on record for the Florida Keys (Manzello 2015), including a prolonged thermal stress event during which water temperatures remained above 30°C for a period of 17 wk at our field site. This thermal event allowed us to test our original questions in the context of environmental extremes predicted to become increasingly common (Hoegh-Guldberg et al. 2007, Descombes et al. 2015). Therefore, we also tested 2 additional questions: (3) Do restored coral genotypes exhibit differences in their response to thermal stress? and (4) Do restored corals demonstrate tradeoffs between growth and survivorship when confronted with thermal stress?

To answer these questions, over the course of 21 mo we tracked the growth and survivorship of experimentally established plots of *Acropora cervicornis* differing in genotypic diversity. We hypothesized that different genotypes would exhibit differences in growth rates and that inter-genotypic competition would suppress growth rates and lead to larger corals in single-genotype treatments compared to those with higher genotypic diversity. Further, we predicted that, at the conclusion of the experiment, survivorship would be highest in the most genotypically diverse plots. Lastly, we hypothesized that genotypes would differ in their response to thermal stress and that genotypes with greater growth rates would demonstrate lower survivorship following thermal stress.

MATERIALS AND METHODS

Study species

Acropora cervicornis is a fast-growing, branching coral species that can rapidly expand via asexual fragmentation (Glynn 1973, Tunnicliffe 1981). The structural complexity provided by *A. cervicornis* and its congener, *A. palmata*, provides essential habitat for a multitude of reef-associated organisms (reviewed in Bruckner 2003). Historically, these 2 species were dominant habitat-forming and reef-building species on many Caribbean reefs, including in the Florida Keys (Hughes 1994, Aronson & Precht 2001). Today, *A. cervicornis* populations on most Caribbean reefs have declined 80 to 90% compared

to 1970s populations, with drastic population reductions of >95% in some areas (Hughes 1994, Aronson & Precht 2001, Bruckner 2003), resulting in significant losses of structural complexity on most Caribbean reefs and their listing as 'Threatened' under the US Endangered Species Act (Hogarth 2006). Currently, coral restoration efforts are primarily focused on *A. cervicornis* due to its life history characteristics amenable to rapid propagation and the species' critical role on Caribbean coral reefs as habitat.

Experimental design

Our field site was a low-relief reef in ~5 to 7 m of water located approximately 10 km offshore of Summerland Key, Florida, USA (24.532° N, 81.483° W). We established 4 experimental blocks of four 1 m^2 plots ≥5 m away from and parallel to the reef ledge. Each block of 1 m^2 plots contained 1 replicate of each genotypic diversity treatment (1-, 2-, 4-, or 6-genotypes). Within each block, 1 m^2 plots were separated by 3 to 4 m, while blocks of 1 m^2 plots were separated by ~30 m. Treatments were randomly assigned to plots within a block. In total, 8 genotypes (named D through K) were used to create experimental treatments; however, due to limited availability of certain genotypes, only 4 genotypes (D, E, F, and G) were present in all treatment levels.

We outplanted 12 colonies of *A. cervicornis*, each approximately 35 cm in total linear extension (TLE), to each plot in May 2013 (Fig. 1). We evenly spaced coral colonies within plots such that colony density and arrangement did not differ between treatments. We also organized colonies to maximize genotype mixing and to avoid clumping of the same genotype in plots with multiple genotypes. Genotype analyses, completed as part of Mote Marine Laboratory's initial establishment of a coral nursery, were done using known microsatellite markers. Corals from confirmed genotypes had been grown in the Mote Marine Laboratory offshore coral nursery from 5 to 10 cm fragments (E. Bartels pers. comm.). We outplanted 4 replicates of each treatment in the randomized block design for a total of 192 corals outplanted into sixteen 1 m^2 plots. Each colony was secured via a cable tie to a masonry nail hammered into the reef substrate and labeled with an individually numbered tag.

Coral colony growth, condition, and predator surveys

To quantify the effects of genotypic identity and diversity on colony growth, we measured coral colony dimensions (length, width, and height) to the nearest cm every 3 to 6 mo. Surveys were conducted in May, September, and December 2013, June and

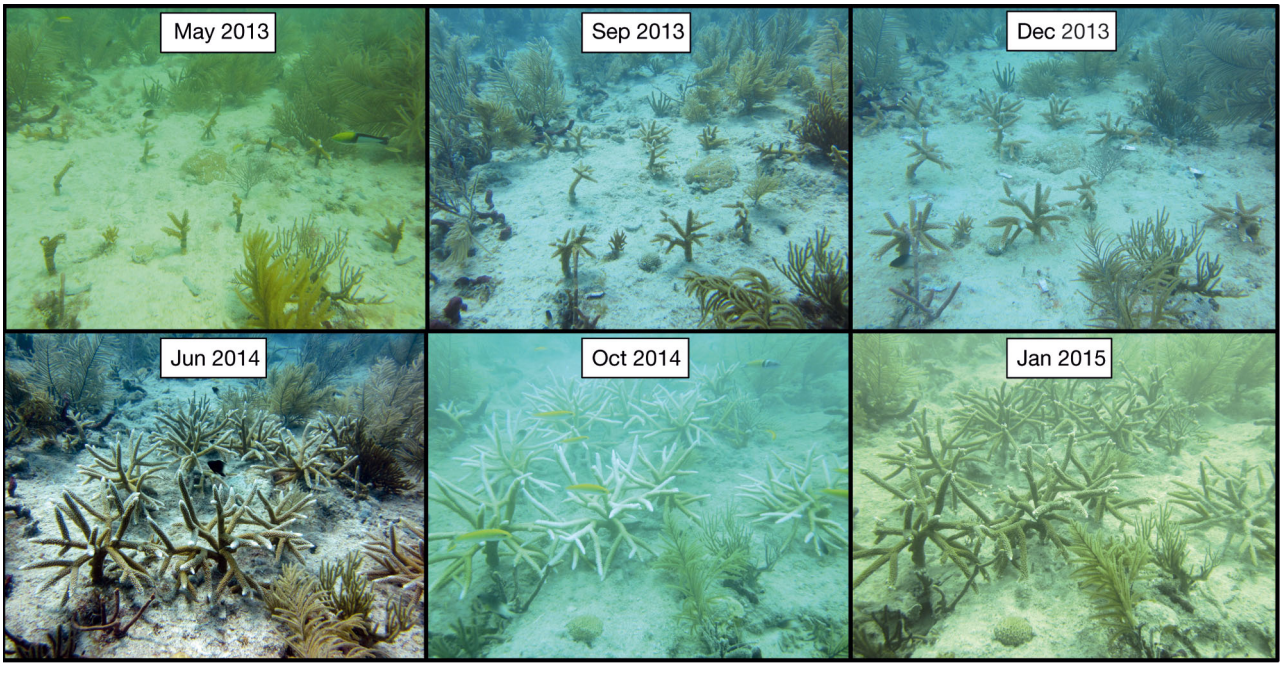

Fig. 1. Photographic time series of an experimental *Acropora cervicornis* plot during each survey period. Bleaching and post-bleaching recovery is evident in October 2014 and January 2015

October 2014, and January 2015 (Fig. 1). At each sampling event, we recorded the percent of each coral colony that contained live tissue, prevalance of coral bleaching, and the presence of disease via visual assessment. We also took a photograph of the entire plot from the same location to compare images through time (Fig. 1). Additionally, we counted corallivorous snails *Coralliophila abbreviata* and fireworms *Hermodice carunculata* on each *A. cervicornis* colony. However, these predators were so rare that we did not explore these data quantitatively.

Beginning 15 June 2014, sea surface temperatures recorded at a site 9 km away at the same depth reached 30°C, just below the threshold for bleaching in *A. cervicornis* (Manzello et al. 2007). Temperatures at this site remained above 30°C from 15 June until 7 October 2014 (see Fig. A1 in the Appendix). During our June 2014 survey (19 June), we did not observe bleaching in any of our experimental *A. cervicornis* corals or naturally occurring coral colonies of any other species growing on the reef at our study site. Therefore, we refer to May 2013 through June 2014 as 'pre-bleaching' surveys. During September and early October 2014, >75% of *A. cervicronis* colonies observed in many areas of the Florida Keys exhibited some degree of bleaching (Manzello 2015). Although we were not able to sample our experiment during the regional height of the bleaching event, we did survey corals again on 30 October 2014 (Fig. 1). While the peak in bleaching at our study site is unknown, at this time corals still exhibited substantial bleaching and we therefore considered this our 'bleaching' survey. Even though we may have missed the peak of the bleaching, the relative patterns in bleaching among genotypes were likely similar to the peak time of bleaching. Our final sampling was conducted in January 2015 for a 'post-bleaching' survey, at which time bleached corals had died or recovered and no bleaching was observed.

Statistical analyses

TLE was calculated using length, width, and height conversions provided by Kiel et al. (2012). Growth rates were calculated for each interval by dividing the TLE accumulated between survey periods by the number of days elapsed to generate a daily growth rate. For all growth rate and TLE calculations, data for corals were not included if they showed signs of breakage that would confound actual coral growth rates. Corals that suffered 100% tissue loss were included in growth rate and TLE calculations for the first survey where total mortality was recorded, but were removed from future growth calculations to avoid artificially depressing growth rates or TLE measures by continually including dead corals in our calculations. Coral colonies were likely broken during natural processes such as turtle and fish activity within plots (M. C. Ladd pers. obs.).

We assessed changes through time in growth rates, TLE, and percent of colony with no live tissue via nested 2-way repeated measures ANOVAs.

Genotypic diversity treatment effects were tested using plot as a replicate by calculating a mean value for the response variable of interest (growth rate, TLE, or percent of colony with no live tissue) for each plot. Treatment effect models considered treatment, survey, and block as fixed factors, with an interaction between treatment and survey and plot considered a random effect.

In separate models, we tested the effect of genotype on individual colony growth rate, TLE, and percent of colony with no live tissue, using a model that considered genotype, survey, and block as fixed factors and included an interaction between genotype and survey. We did not include genotypic diversity treatment in this model because only a subset of genotypes were present in each treatment making it impossible to test for effects of both genotypic diversity and genotypic identity in the same model. In models testing for effects of genotype, individual corals were nested within a plot and considered as a random effect to avoid violating assumptions of independence. When there were significant genotypic diversity or genotype effects, we tested for differences among treatment or genotype for individual survey periods via post hoc tests with Tukey's corrections using the 'multcomp' package in R (Hothorn et al. 2008). Among-genotype differences in percent of colony bleached were assed via an ANOVA using the October 2014 survey period. Growth rates, percent of colony with no live coral tissue, and percent of colony bleached were square-root transformed to meet ANOVA assumptions.

Survivorship within genotypic diversity treatments was calculated using the percentage of colonies that were alive within a plot at each survey period. A coral was considered dead when it had no living tissue on the skeleton. Among-treatment differences in survivorship at the end of the experiment (January 2015) were analyzed using an ANOVA with treatment and block as fixed factors. Survivorship among genotypes was calculated as the percentage of coral colonies for each genotype that remained alive at a given survey point. Among-genotype differences in

survivorship at the end of the experiment were analyzed via a Fisher's exact test, followed by pairwise comparisons of the 8 genotypes using a Bonferroni correction.

To determine if there was a relationship between growth rate and final TLE, tissue loss, or bleaching prevalence, we regressed the average growth rate for each genotype from September to December 2013 against the mean final TLE, percent of colony with no tissue at the conclusion of the experiment, or percent of colony bleached in October 2014. We used growth data from September to December 2013 (henceforth referred to as 'initial' growth rates) to represent individual genotype growth rates. Focusing on this time period removed any influence from transplant stress (May to September 2013). Using data from this time period also removed any influence of intraspecific competition, which can influence coral growth rates and was observed after our December 2013 survey (Chadwick & Morrow 2011, Griffin et al. 2015). All analyses were conducted in R version 3.0.2 (R Core Team 2013).

Table 1. Nested 2-way repeated-measures ANOVA testing (a) genotypic diversity treatment effects and (b) genotype effects on *Acropora cervicornis* growth rate, total linear extension, and percent of colony without live tissue. **Bold** values indicate significance at $p < 0.05$

Response variable	Predictor	df	*F*	p
(a) Genotypic diversity effects				
Growth rate (cm d^{-1})	Survey	5,59	27.15	**<0.001**
	Treatment	3,9	0.25	0.86
	Treatment × survey	15,59	0.71	0.77
	Block	3,9	1.77	0.22
Total linear extension	Survey	5,59	38.55	**<0.001**
	Treatment	3,9	0.30	0.82
	Treatment × survey	15,59	0.34	0.99
	Block	3,9	1.27	0.34
Percent of colony without live tissue	Survey	5,47	29.02	**<0.001**
	Treatment	3,9	0.52	0.68
	Treatment × survey	15,47	0.28	0.99
	Block	3,9	0.69	0.58
(b) Genotype effects				
Growth rate (cm d^{-1})	Survey	5,642	340.78	**<0.001**
	Genotype	7,169	0.63	0.73
	Genotype × survey	35,642	2.26	**<0.001**
	Block	3,12	2.67	0.09
Total linear extension	Survey	5,585	700.51	**<0.001**
	Genotype	7,169	2.35	**0.026**
	Genotype × survey	35,585	4.99	**<0.001**
	Block	3,12	3.47	0.06
Percent of colony without live tissue	Survey	5,905	276.16	**<0.001**
	Genotype	7,169	6.21	**<0.001**
	Genotype × survey	35,905	5.75	**<0.001**
	Block	3,12	0.62	0.61

RESULTS

Genotypic diversity effects

Genotypic diversity within plots had no effect on coral growth rates (treatment effect: $F_{3,9} = 0.247$, $p = 0.86$) or TLE (treatment effect: $F_{3,9} = 0.303$, $p = 0.82$) during any survey period in the experiment (Table 1). Genotypic diversity treatments also had no effect on bleaching prevalence within plots ($F_{3,9} = 0.486$, $p = 0.70$) or mean percent of colony with live tissue (treatment effect: $F_{3,9} = 0.52$, $p = 0.68$).

Genotype effects

Mean growth rates among genotypes ranged 4-fold, from a minimum of 0.18 to a maximum of 0.73 cm d^{-1} (mean ± SE: 0.33 ± 0.01 cm d^{-1}) and significantly differed through time among genotypes (genotype × survey effect: $F_{35,642} = 2.256$, $p < 0.001$; Fig. 2a). However, post hoc tests with Tukey's correction were unable to detect significant differences in growth rates among genotypes, likely due to the high number of comparisons conducted. Mean daily growth rates for genotype D nearly tripled after the 2014 thermal stress event (from 0.25 to 0.73 cm d^{-1}), and manifested in a large increase in mean TLE, a proxy for habitat produced (genotype × survey effect: $F_{35,585} = 4.998$, $p < 0.001$; Fig. 2b). We found that individuals of genotype D were on average 20 to 327% larger than the other genotypes by the end of the experiment.

After the thermal stress event, during the October 2014 survey we observed significant differences among genotypes in the percent of coral colonies bleached ($F_{7,166} = 4.77$, $p < 0.001$; Fig. 3). Specifically, genotype D and K corals had on average nearly twice the amount of bleached coral tissue per colony compared to all other genotypes.

Genotypic differences in response to the thermal stress event were evident in cumulative survivorship, which varied 3-fold among genotypes (Fisher's exact test, $p < 0.001$; Fig. 4a) and ranged from a high of

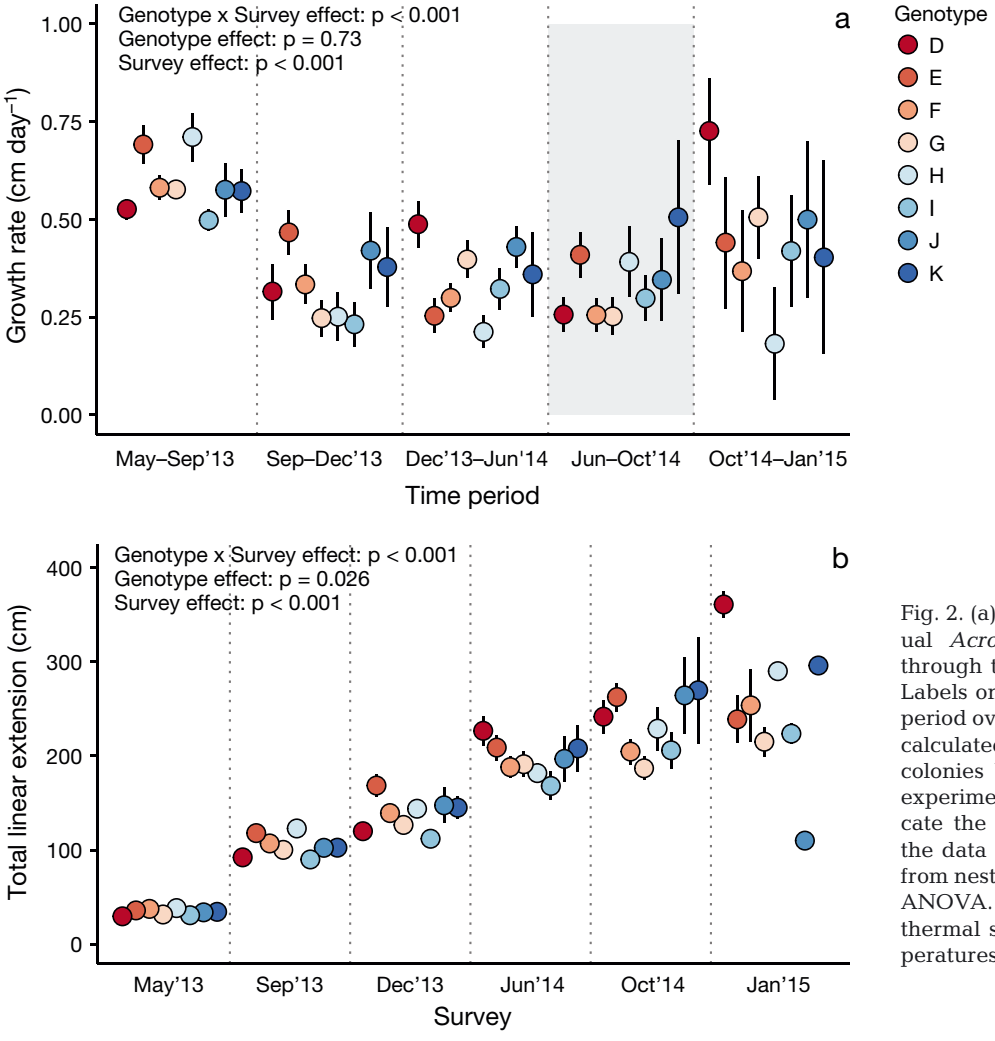

Fig. 2. (a) Daily growth rate of individual *Acropora cervicornis* genotypes through time regardless of treatment. Labels on the *x*-axis indicate the time period over which the growth rate was calculated. (b) Total linear extension of colonies by genotype throughout the experiment. Labels on the *x*-axis indicate the survey period during which the data were collected. Statistics are from nested 2-way repeated-measures ANOVA. Shaded area: 17 wk period of thermal stress when sea surface temperatures remained above 30°C. Data are means ± SE

93.1% to a low of 27.8% of colonies remaining alive at the end of the experiment. There was no effect of genotypic diversity treatment on cumulative survivorship (treatment effect: $F_{3,9} = 0.06$, p = 0.98). Thermal stress appeared to drive differences between genotypes in the average percent of a colony with no live tissue at the end of the experiment (genotype × survey effect: $F_{35,905} = 5.75$, p = < 0.001; Fig. 4b). By October 2014, genotypes E, F, and J had lost live tissue on approximately 3× more of the skeleton per colony compared to genotypes D, G, and I. This pattern held until the end of the experiment, suggesting there was little tissue recovery after the bleaching event for these genotypes. All results from nested 2-way repeated measures ANOVAs can be found in Table 1.

We found no relationship between mean initial growth rates (September to December 2013) and final TLE ($F_{1,6} = 0.513$, p = 0.54) across genotypes (Fig. 5a). Thus, initial growth rates were not related

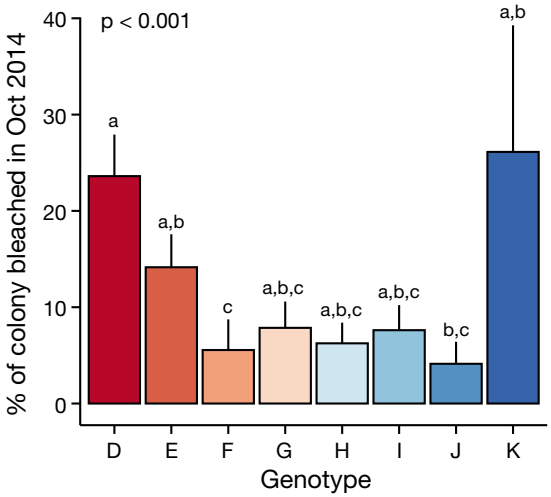

Fig. 3. Mean (+SE) percent of colony bleached in October 2014 for the 8 *Acropora cervicornis* genotypes used in this study. Statistics are from 1-way ANOVA. Different letters represent significant differences (p < 0.05) among genotypes from post hoc tests with Tukey's correction

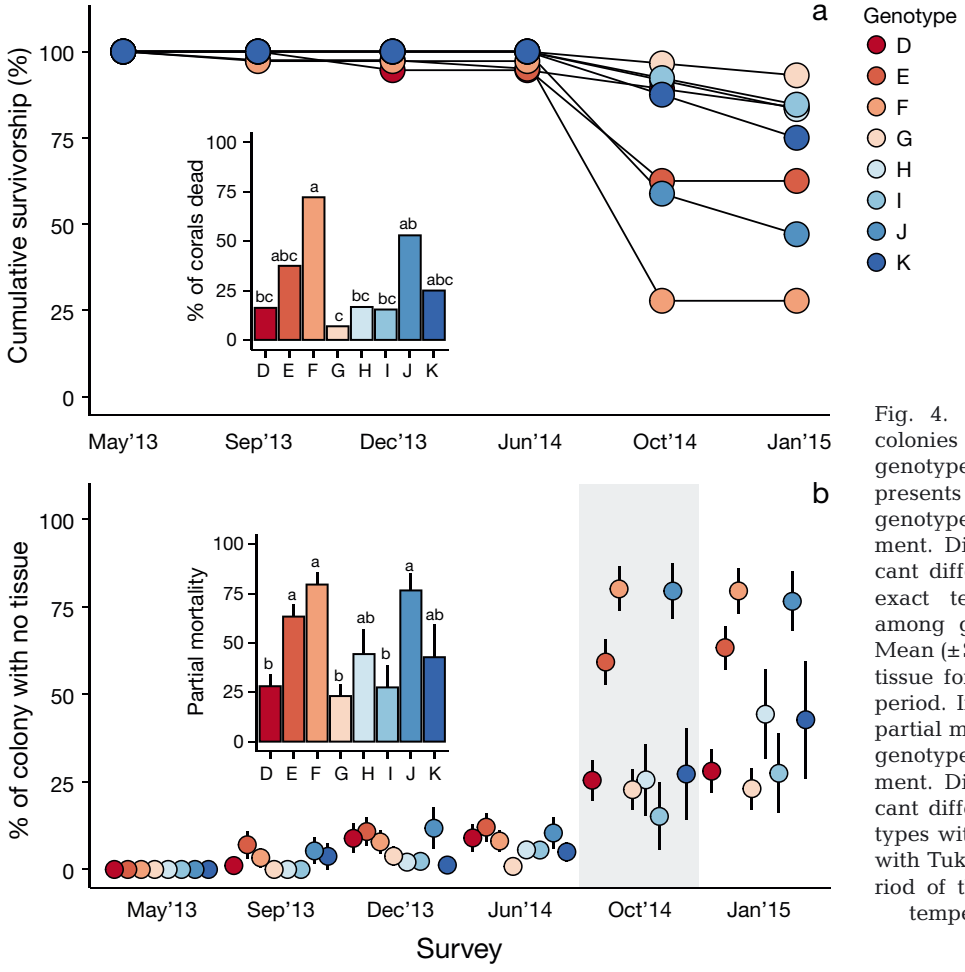

Fig. 4. (a) Cumulative survivorship of colonies of the 8 *Acropora cervicornis* genotypes used in this study. Inset bar plot presents percent of corals dead for each genotype at the conclusion of the experiment. Different letters represent significant differences ($p < 0.05$) from Fisher's exact test with Bonferroni correction among genotypes in January 2015. (b) Mean (±SE) percent of colony without live tissue for each genotype at each survey period. Inset bar plot presents the mean partial mortality per coral colony for each genotype at the conclusion of the experiment. Different letters represent significant differences ($p < 0.05$) among genotypes within a survey from post hoc tests with Tukey's correction. Shaded area: period of thermal stress when sea surface temperatures remained above 30°C

to final amount of habitat created. Similarly, there was no relationship between initial growth rates and the amount of bleached tissue in coral colonies ($F_{1,6}$ = 0.417, p = 0.542). However, the percent of tissue on a colony that died during the experiment was significantly positively related to initial genotype-specific growth rates ($F_{1,6}$ = 6.445, p = 0.044; Fig. 5b), indicating that genotypes with faster initial growth rates ultimately lost more live tissue.

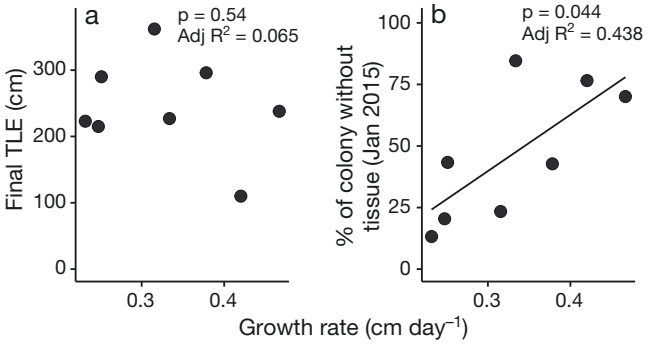

Fig. 5. Mean growth rate for each *Acropora cervicornis* genotype from October to December 2013 regressed against (a) mean total linear extension (TLE) for each genotype and (b) mean percent of colony with no live tissue at the end of the experiment in January 2015. Statistics are from linear regression

DISCUSSION

Coral restoration is gaining traction globally as a feasible approach to restore degraded reefs on a local scale (Montoya-Maya et al. 2016). Understanding how restored corals will perform when outplanted to degraded reef sites, particularly in response to common stressors, is an important step towards developing more effective restoration strategies. Our study revealed important genotype-specific differences among restored corals in growth and survivorship, key elements of successful coral restoration. We found a 4- and 3-fold difference in growth rates and survivorship, respectively, and up to 327% difference in the amount of habitat created by corals of different genotypes. Further, these differences were context-dependent and only emerged after a prolonged (17 wk) thermal stress event that induced

coral bleaching and mortality. Importantly, genotypes with faster initial growth rates suffered more tissue mortality after the bleaching event. To our knowledge, this is the first example of tradeoffs in performance between important traits in corals used for restoration.

Our work adds to a growing body of literature suggesting that the genotypic identity of corals should be a key factor to consider when planning coral restoration efforts (Jin et al. 2016). We found a nearly 3-fold difference in growth rates among genotypes during our 21 mo study. Previous work with nursery-raised *Acropora cervicornis* has demonstrated variable growth rates based on genotype and source location (Bowden-Kerby 2008, Griffin et al. 2012), manifesting in variable growth rates for corals outplanted to coral reef sites (Lirman et al. 2014). However, most studies documenting the performance of restored corals have been on relatively short time scales (≤1 yr), often in an ideal setting such as an underwater nursery, and averaged growth rates over the entire study period (e.g. Griffin et al. 2012, Lirman et al. 2014). Our results are unique in that our experiment was in a natural reef setting where the different genotypes were subjected to the normally occurring biotic and abiotic forces on reefs that can shape differential growth and survivorship. Further, our longer time scale allowed us to examine how prolonged thermal stress, which will likely become more common with global climate change (Hoegh-Guldberg et al. 2007, Descombes et al. 2015), differentially impacts genotypes of corals used for restoration.

One of the major goals of coral reef restoration is to restore the ecological processes and feedbacks that can drive community recovery. One key driver of these positive feedbacks on reefs is the creation of structural complexity by live coral (Mumby & Steneck 2008), which provides habitat for diverse and ecologically important fish and invertebrate assemblages (Newman et al. 2015), refuge from predators (Almany 2004), and facilitates nutrient cycling (Holbrook et al. 2011, Shantz et al. 2015). Surprisingly, we found no relationship between initial growth rates and the amount of habitat produced by a coral. This finding suggests that initial growth rates, often used to evaluate corals raised in nurseries (e.g. Griffin et al. 2012, Lirman et al. 2014), may not be a reliable predictor for how corals will perform when outplanted for restoration. Further, coral genotypes with initially high growth rates ended up losing more live tissue after the thermal stress event than colonies with slower initial growth rates, suggesting a tradeoff between growth rate and ability to cope with thermal stress. Another potential explanation for this tradeoff could be differences in energy allocation strategies between coral genotypes. Coral energy reserves are positively correlated with survival and recovery from bleaching events (Grottoli et al. 2014, Schoepf et al. 2015). However, calcification is an energetically intensive process. Thus, genotypes that devote more energy to rapid growth may possess smaller energy reserves than slower-growing genotypes, resulting in less capacity to deal with stressors.

In the Pacific, coral families with the highest skeletal extension rates often have lower immunity levels compared to those with lower growth rates (Palmer et al. 2010). Similarly, in our study the 3 genotypes with the lowest initial growth rates displayed roughly 3× less tissue loss than genotypes with faster initial growth rates. There could also have been a positive relationship between growth rate and bleaching prevalence that we did not detect if we indeed missed the peak of the bleaching event. Importantly, the tradeoff between growth and tissue loss after thermal stress was evident with only 8 genotypes. Had we been able to include a higher number of genotypes with a wider range of traits, we may have seen stronger or more diverse tradeoffs.

Corals can exhibit high levels of local adaptation, including the ability to cope with a variety of stressful conditions (Barshis et al. 2010, Sanford & Kelly 2011). Such differences among genotypes suggest that genotype–environment interactions are likely important to consider in restoration-planning to maximize the survival and growth of restored corals. Our findings suggest that numerous tradeoffs likely exist among multiple coral traits, highlighting the need to test genotypes across a range of environmental conditions. For example, genotypes of *A. cervicornis* differ in disease resistance (Vollmer & Kline 2008), thermal tolerance (this study), growth rates (Griffin et al. 2012), and habitat production (this study). Given such differences, we predict tradeoffs among these traits to influence the performance of restored corals when exposed to stressors such as thermal tolerance or disease (Fig. 6). Understanding the performance of restored corals under varied biotic and abiotic conditions is particularly relevant in a time of global climate change that will see an increase in both chronic and acute stressors on many coral reefs (Descombes et al. 2015, Gattuso et al. 2015, Pendleton et al. 2016).

Genotypic diversity of foundation species can be a major driver of community structure and ecosystem function (Crutsinger et al. 2006). However, we found that genotypic diversity had no effect on the growth

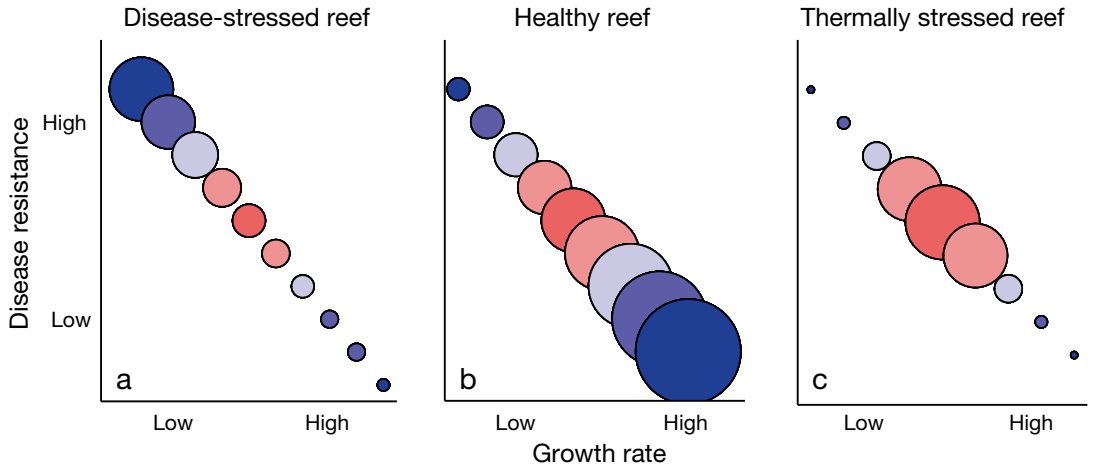

Fig. 6. Visualization of a potential tradeoff among multiple coral traits under different environmental contexts. Each circle represents a distinct coral genotype. Cooler colors represent thermally intolerant genotypes, while hotter colors represent thermally tolerant genotypes. The amount of habitat created by a genotype is depicted by the size of each circle, with smaller circles representing less habitat created compared to larger circles. Genotype-specific growth rates (*x*-axis), disease resistance (*y*-axis), and thermal tolerance (color) may all interact to influence the amount of habitat generated by restored corals. Habitat generation by restored corals will be highly influenced by environmental context and tradeoffs among important coral traits. Shown are hypothesized outcomes at a site heavily influenced by coral disease (a) and a site subjected to thermal stress (c) as compared to a relatively healthy reef (b)

rate, size, or survivorship of restored *A. cervicornis*. The unexpected lack of a genotypic diversity effect on restored coral performance may have been due to several factors. Restricted availability of specific genotypes limited our highest genotypic diversity treatment to 6 genotypes, while genotypic diversity effects may be evident only at higher levels of genotypic diversity. However, the prominence of asexual fragmentation by *A. cervicornis* (Tunnicliffe 1981) and extremely low sexual recruitment in the Florida Keys (van Woesik et al. 2014) suggest that our genotypic diversity treatments were within realistic ranges for natural populations. Diversity effects may be emergent properties only evident at the level of ecosystem processes such as primary production or nutrient cycling and not detectable by measuring growth and survivorship responses in individual corals. Alternatively, specific genotype combinations may be required to generate hypothesized genotypic diversity effects. For example, in rocky intertidal seaweed communities, biodiversity can enhance nitrate uptake and photosynthesis, but only in realistic (non-random) assemblages (Bracken & Williams 2013). Thus, it is plausible that the genotypic composition of restored coral populations is as important, if not more, than genotypic diversity for restoration success.

The need for coral restoration is becoming increasingly urgent as the worlds' reefs continue to lose corals (De'ath et al. 2012, Jackson et al. 2014, Graham et al. 2015, Hughes et al. 2017). It is critical to recognize that environmental conditions are variable across reefs and over space and time. Thus, matching genotype-specific performance to the environmental conditions of restoration sites will be critical to furthering restoration goals. We suggest weighting restoration at sites with predictable conditions towards genotypes with known attributes that can boost survivorship and habitat production. Conversely, at sites prone to frequent disturbances or highly variable conditions, including a suite of traits from numerous genotypes at a single restoration site may be important to maximize the likelihood that these populations will persist under uncertain future conditions (Pandolfi 2015, Pendleton et al. 2016). Ultimately, long-term studies assessing how different genotypes perform under a variety of environmental conditions will afford restoration practitioners the ability to select genotypes best suited for site-specific conditions and increase the chances of achieving restoration goals.

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Appendix

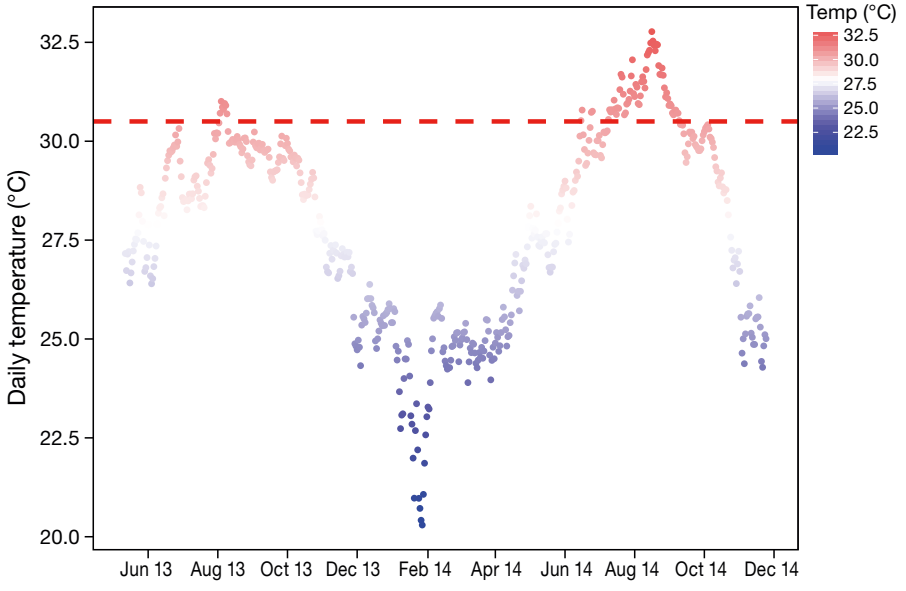

Fig. A1. Daily water temperature recorded at a site 9 km away from our study area, at similar depth. Red dashed line: bleaching threshold (30.5°C) for *Acropora cervicornis* according to Manzello et al. (2007)

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