

Impacts of fragment genotype, habitat, and size on outplanted elkhorn coral success under thermal stress

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ABSTRACT: Active coral restoration through coral ‘gardening’ aims to remediate some of the drastic coral cover lost on Caribbean reefs, with increasing attention to the imperiled, iconic foundation species elkhorn coral *Acropora palmata*. We documented 2 experiments quantifying effects of *A. palmata* outplant characteristics and habitat on outplant success. Two thermal stress events (summer 2014 and 2015) occurred while the experiments were underway and thus lend insight into environmental interactions and coral restoration outcomes under projected thermal regimes. In the first experiment comparing 2 size classes of a single genotype, smaller fragments produced significantly more live tissue area, experienced less bleaching, and demonstrated equal survivorship compared to larger fragments. The second experiment compared 4 genotypes outplanted to both fore reef and mid-channel patch reef habitats. Genotypes varied significantly in survivorship, bleaching severity, and net change in size, with one (CN2g) performing well in all 3 metrics, and another (SLg) exhibiting poor survivorship, the most bleaching, and smaller changes in size. Overall, bleaching was less severe and survivorship less varied between genotypes in fore reef versus patch reef habitats. Fragments returned to the site of genotype origin did not consistently outperform ‘foreign’ genotypes from a different habitat type. Recognizing unique attributes associated with size and specific genotypes may improve the efficacy of active coral restoration in the face of future climate scenarios.

KEY WORDS: *Acropora palmata* · Genet · Bleaching · Transplant · Local adaptation · Florida Keys

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INTRODUCTION

As Caribbean coral cover declined through the final decades of the 20th century (Jackson et al. 2014), solutions were sought to replace Caribbean reef coral structure. Live coral produces framework, undergirding ecosystem services by providing shoreline protection, harboring diverse organisms through varying life stages, and regulating biogeochemical cycles (Moberg & Folke 1999). ‘Coral gardening’ (Rinkevich 2005), wherein wild fragments are collected, propagated in common-garden *in situ* nurseries, and then ‘outplants’ transplanted to the reef, has become an increasingly popular tool to combat the ongoing degra-

dation of reefs. Outplanting of foundation Caribbean elkhorn and staghorn corals (*Acropora palmata* and *A. cervicornis*) has been widely implemented across the Caribbean (Young et al. 2012) and in the Florida Keys as a necessary recovery action under the US Endangered Species Act recovery plan (National Marine Fisheries Service 2015). *A. cervicornis*, with high growth rates and ease of fragmentation, is the target of most current restoration efforts, including considerable investigation of the influence of coral traits, outplant configuration, and location on success (Griffin et al. 2015, Mercado-Molina et al. 2015, Ladd et al. 2016, 2017, Drury et al. 2017). The larger and more robust elkhorn coral *A. palmata* is being increasingly tar-

geted in coral gardening efforts, but little investigation has addressed factors affecting its outplant success.

Historically prolific in the upper Florida Keys (Precht & Miller 2007), by the early 2000s *A. palmata* cover had declined by more than 95% from previous abundances (Miller et al. 2003), with rapid declines continuing since then (Williams et al. 2014b, Sutherland et al. 2016). Important drivers of *A. palmata* mortality include storms, disease, predation by the corallivorous snail *Coralliophila abbreviata* (Williams & Miller 2012), as well as acute thermal bleaching events (Williams et al. 2017). Rising global temperatures pose an ongoing threat, as the Florida reef tract is projected to experience severe annual thermal bleaching by 2040, and other regions of the Caribbean as early as 2030 (van Hooidonk et al. 2015). While common habitat of existing *A. palmata* is in shallow fore reef and reef crest habitats, surprisingly robust populations, including thriving thickets, are found in alternate environments in the upper Florida Keys (Miller et al. 2008) including mid-channel patch reefs and along back reef fringes behind the reef crest. These stands are often sheltered from wave energy and surrounded by shallow water resulting in greater fluctuations in temperature, particularly in summer when solar radiation warms the surrounding water. Fore reef populations are at the shelf margin where they are exposed to relatively greater mixing with deeper offshore water that likely serves as a buffer from extreme temperature fluctuation.

Genotypic diversity in wild *A. palmata* stands is variable across its range (Baums et al. 2006), but in the upper Florida Keys it is particularly low, and declining (Williams et al. 2014b). Consequently, preserving or enhancing genotypic diversity is a priority of active coral restoration in the region. While all genotypes contribute to reef-wide diversity and sexual reproductive potential, certain genotypes may possess traits more favorable for outplanting (e.g. resistance to transplant stress, accelerated growth rate), or may be better suited for certain habitats or reef of origin (Baums 2008).

Basic principles of restoration genetics suggest that individual organisms will perform best in habitats most similar to their native habitat (i.e. local adaptation). This principle is generally operationalized by management agencies by discouraging translocation over long distances, or to areas where some level of genetic connectivity with the native sites is not evident (e.g. Florida Fish and Wildlife Conservation Commission 2007). Existing evidence for local adaptation in corals is ambiguous, with both locally adapted and generalist genotypes described, sometimes

within a single species (Smith et al. 2007, Vermeij et al. 2007, Drury et al. 2017). High clonality in some *A. palmata* has been cited as evidence of local adaptation of highly replicated genotypes (Baums 2008). However, rapid climate and other environmental changes ongoing in coastal habitats raise the possibility that historically adapted genotypes may experience a disparity with their local environment. This phenomenon suggests an alternate restoration strategy using non-local genotypes that are adapted to future, rather than present, conditions at a restoration site (so called 'predictive provisioning'; Jones 2013, Williams et al. 2014a).

Further investigation of the effects of fragment genotype and outplant location on overall fragment success is of interest to coral population enhancement efforts, as these are factors that can be controlled and ideally optimized during outplanting efforts. Size of fragment at time of outplanting may also be controlled for with differing levels of propagation investment. Elkhorn coral is one of the fastest growing species in the Caribbean, yet twice as many fragments can be produced per year if they are outplanted, for example, after 6 mo nursery propagation time rather than 1 yr. This motivated our investigation into the performance of 2 size classes that are realistically feasible for nurseries to grow on a large scale. Better, or equal, performance by relatively smaller fragments can improve restoration efficiency by reducing the time and effort required to produce larger fragments.

Here, we report the results of 2 experiments: one testing the effect of outplanted fragment size and the second testing performance of 4 genotypes outplanted to 2 distinct habitat types. We hypothesized that large fragments would exhibit both greater net increase in size and higher survivorship than small fragments, due to the larger circumference of growing margins (at the base and branch tips) and greater surface area allowing for increased resilience to partial mortality from predators and disease. If *A. palmata* genotypes are finely adapted to their native habitat or site, we would expect that individual genotype performance would depend on habitat, and 'native' genotypes should outperform transplants at a given site or habitat type. Serendipitously, these experiments coincided with extreme summer thermal stress events in both 2014 and 2015. Hence, the experiments provided comparisons of the effects of size, genotype, and outplant habitat on fragment performance under elevated thermal stress which, though anomalous when compared with historical records, may represent the norm in coming decades.

MATERIALS AND METHODS

Size experiment

Two size treatments, 'large' and 'small' *Acropora palmata* fragments, were outplanted in pairs 1 m apart across 3 replicate fore reef sites in May 2014. Hereafter, 'outplants' and 'fragments' are used interchangeably, with $n = 126$ pairs. Due to the irregular morphology and common partial mortality of *A. palmata* fragments, a live area index (LAI) was used in this study as a proxy for size. LAI was calculated as the square of the average of length, width, and height, multiplied by the proportion of live tissue cover (Williams & Miller 2012). Large fragments averaged $108 \pm 27 \text{ cm}^2$ (mean \pm SD) LAI with average length and width dimensions of 14 and 9 cm, respectively. This size represents a fragment cohort requiring 9 to 12 mo in-nursery propagation time (K. Ripple pers. comm.). Small fragments, resulting from 6 to 9 mo propagation time, averaged $51 \pm 14 \text{ cm}^2$ LAI, with average length and width of 10 and 6 cm, respectively. All fragments were propagated from a single genotype, named SLg (see below), by the Coral Restoration Foundation (CRF) in an *in situ* nursery and then attached to cleared reef substrate with 2-part underwater epoxy.

We targeted outplant locations of similar depth where *A. palmata* previously existed, as indicated by remnant skeletons. Depths of outplants were approximately 6 m at French (FR) reef, 5 m at Molasses (ML) reef, and 4.5 m at Pickles (PI) reef. The outplant and source site coordinates are provided in Table S1 in the Supplement at www.int-res.com/articles/suppl/m592p109_supp.pdf. Full surveys to measure size and condition were conducted in June 2014 (initial), November 2014, June 2015, and December 2016 (final). Due to severe thermal heat stress and concurrent bleaching that occurred from July to September 2014, two additional 'condition-only' surveys were conducted in August and September 2014. Condition metrics included a visual estimate of percent live tissue cover, bleaching severity, and presence/absence of the corallivorous snail *Coralliophila abbreviata* on the fragment. For each fragment alive at the final survey, the number of surveys in which snails were present was averaged to give a mean snail presence score for each fragment. Bleaching severity was quantified as an ordinal score with 0 = none, 1 = pale coloration of part of the fragment, 2 = pale coloration of >90% of fragment, 3 = bleached white over part of fragment, or 4 = bleached white over >90% of fragment. Size was measured *in situ* as length (longest dimension),

width (axis perpendicular to length) and height. Growth, including both expansion and partial mortality (i.e. net change in size), was measured as the change in LAI over the whole experiment, reported only for fragments with >0% live tissue cover at the final survey.

Genotype experiment

Multilocus genotypes were determined via micro-satellite markers (Baums et al. 2005) when coral fragments were harvested and brought into nursery culture. Genotypes were tracked carefully throughout nursery propagation according to best practices (Johnson et al. 2011). Four genotypes were chosen for the experiment based on abundant availability from CRF's early nursery culture effort. The Horseshoe genotype (HSg, with 'g' denoting genotype name as opposed to outplant site) originated from a mid-channel patch reef. Snapper Ledge (SLg) and Conch Reef 2 (CN2g) were first collected from a fore reef location, and Conch Reef 1 (CN1g) originated from a more protected habitat behind the fore reef (i.e. back reef). All 4 genotypes were outplanted from nursery propagation in May 2015. The 2 habitat treatments included mid-channel patch reef and wave-exposed fore reef, with 3 replicate sites of each habitat. Patch reef sites, including AAA (AA), Horseshoe (HS), and North Dry Rocks (ND), were approximately 3.5 m in depth. Fore reef sites ranged 4.5 to 6 m in depth and were the same sites from the size experiment (Table S1). A total of 30 fragments of approximately equal size ($40 \pm 15 \text{ cm}^2$) of each of the 4 genotypes ($n = 120$) were outplanted to each of the 6 sites, totaling 720 outplants. Fragments were assessed as described above for the size experiment in surveys conducted early June, mid-July, and November 2015, and June and December 2016. Additional condition-only surveys were conducted in September and October 2015 to assess response to the thermal stress during fall 2015.

Statistical analyses

All data analyses were carried out using JMP v.13 except for survivorship, which was analyzed using SPSS v.24 Wilcoxon survival analysis. Sizes were compared within each site and genotypes within each site and habitat. To compare peak bleaching scores (i.e. scores of the survey when bleaching was most severe) in the size experiment, a 2-factor ordi-

nal logistic model tested the fixed effects of site and size, as well as interaction. The same factors were used in a fixed effects model for change in LAI and average ranked mean snail presence in the size experiment. In the genet experiment, 3-factor nested effect models tested the effect of genotype, outplant habitat, and site nested within habitat, as well as the genotype × habitat interaction. These same factors were used in testing the ordinal bleaching scores in an ordinal logistic model. Holm-Sidak or Tukey-Kramer post hoc pairwise comparisons were conducted between levels of significant factors. The raw dataset is archived online (Miller & Williams 2017).

RESULTS

Size experiment

Separate Wilcoxon survival analyses showed no significant differences in survivorship between the large and small sized fragments within any of the 3 sites over the 2.5 yr period, with 25 and 26% survivorship respectively across sites (Fig. 1a). However, fragments at FR reef had almost triple the survivorship of those at PI reef (43 vs. 15%) with ML reef intermediate (22%; see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m592p109_supp.pdf).

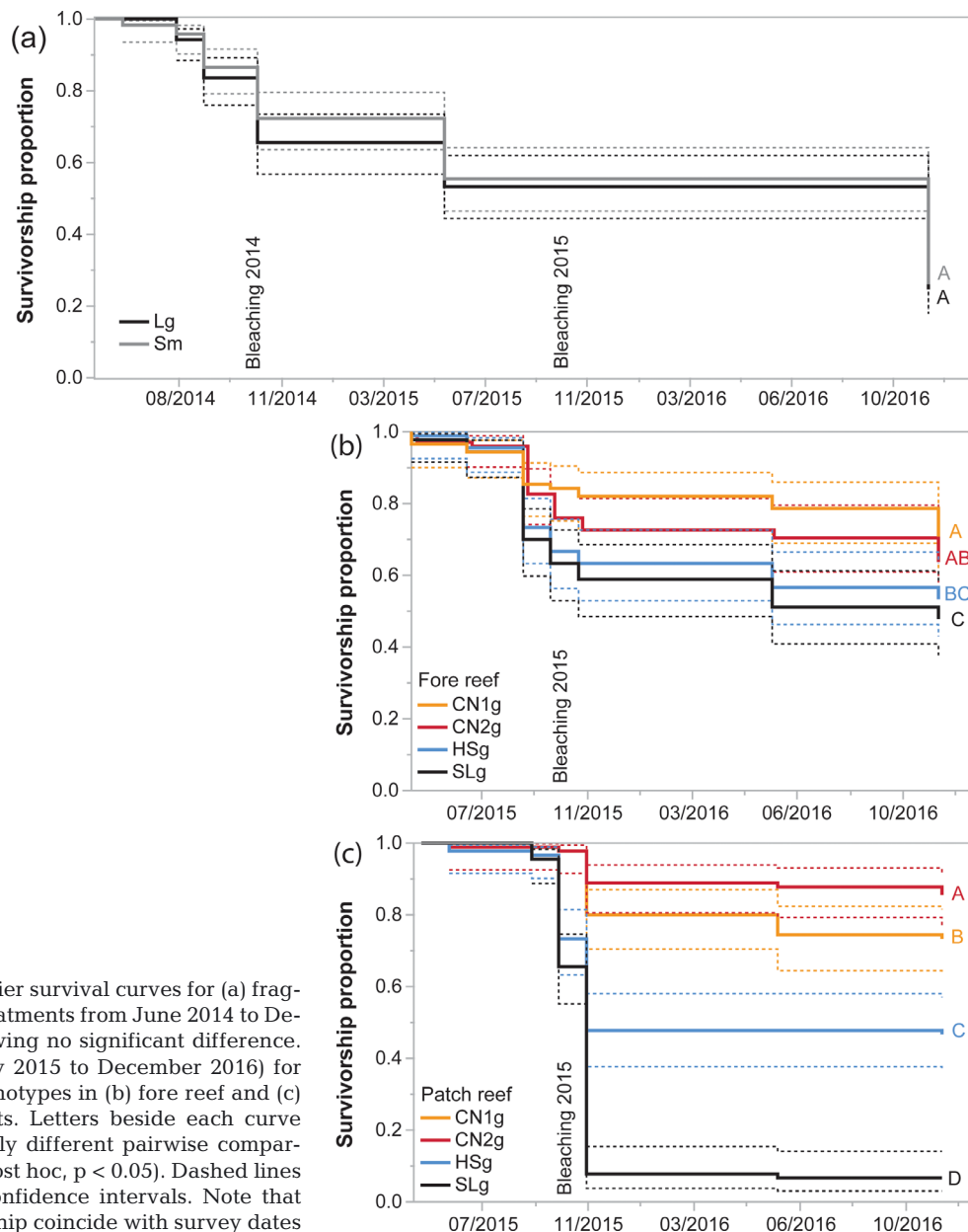


Fig. 1. Kaplan-Meier survival curves for (a) fragments of 2 size treatments from June 2014 to December 2016 showing no significant difference. Survivorship (May 2015 to December 2016) for fragments of 4 genotypes in (b) fore reef and (c) patch reef habitats. Letters beside each curve denote significantly different pairwise comparisons (Wilcoxon post hoc, $p < 0.05$). Dashed lines represent 95% confidence intervals. Note that drops in survivorship coincide with survey dates

Bleaching scores during the peak of bleaching in September 2014 were significantly different between sites (logistic ordinal regression; $\chi^2_2 = 72.2$, $p < 0.001$; Fig. 2a) and sizes ($\chi^2_1 = 4.68$, $p = 0.031$), with no significant interaction. Unexpectedly, small fragments bleached significantly less than large fragments, a pattern most apparent at ML reef although it experienced the least bleaching of all sites. Fragments at PI reef were the most severely bleached. Over the 30 mo experiment, small fragments added a significantly greater increment of LAI (214 ± 34 cm², mean \pm SE) than did large fragments (103 ± 37 cm²; $F_{1,55} = 5.75$, $p = 0.020$; Fig. 3a). Site did not have a significant effect on change in LAI.

Overall, snails were found on 7% of outplants alive at the end of the experiment, ranging from 16% at PI reef to 2% at FR reef across surveys. The mean snail presence on fragments was marginally different among sites ($F_{2,55} = 3.05$, $p = 0.055$) but size was not significant.

Genotype experiment

At each fore reef and patch reef site, significant differences in survivorship were found among the 4 genotypes (all $p < 0.03$), except for FR reef ($p = 0.125$), a fore reef site. Genotype survivorship

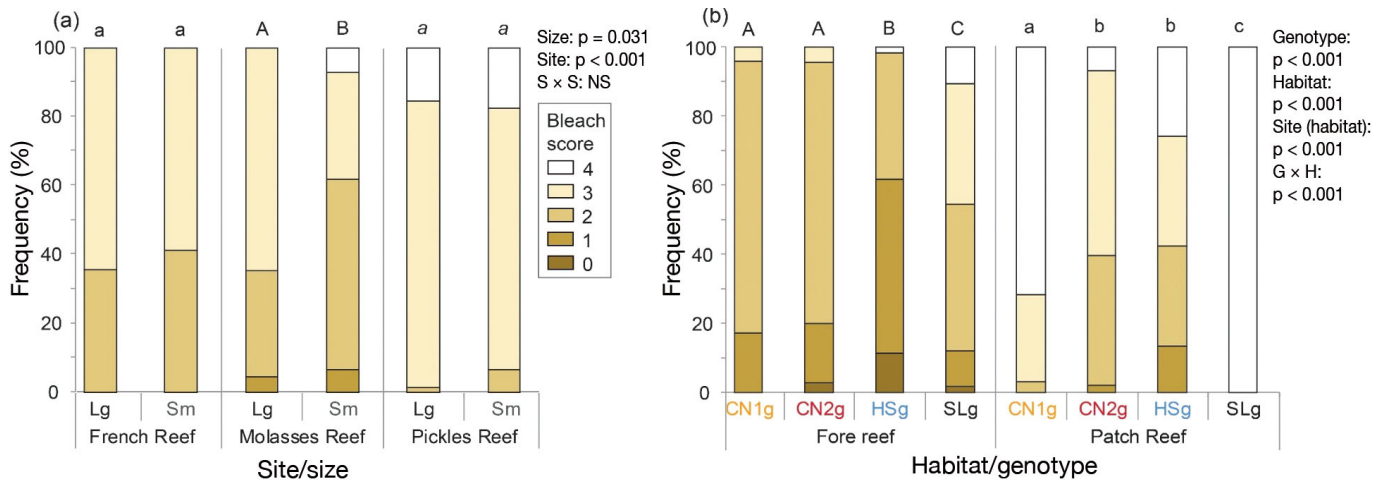


Fig. 2. Frequency of peak bleaching scores as percentage of live fragments in the (a) size (Sept 2014) and (b) genotype (Oct 2015) experiments. Sites within each habitat (b) are pooled. Bleaching score colors range from dark brown, representing 0 (no bleaching), to white or 4 (>90% of the fragment completely bleached). Different letter cases or *italics* denote groups within which pairwise comparisons (Tukey-Kramer post hoc, $p < 0.05$) were performed

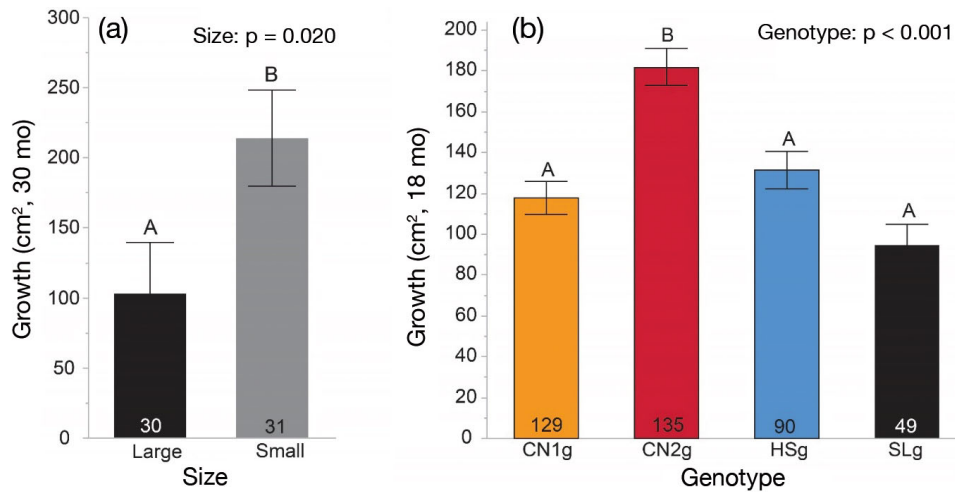


Fig. 3. Change in live area index (LAI; cm²) for duration of (a) size experiment and (b) genotype experiment. Error bars: one standard error of the mean. Number of live fragments at end of experiment (n) shown in each bar. Genotypes and sizes with different letters differed significantly (Tukey-Kramer post hoc, $p < 0.05$)

rankings were nearly identical among sites within habitat types (Fig. S2) and are thus pooled in Fig. 1. At fore reef sites, CN1g fragments exhibited the highest survivorship at 70%, a level not significantly greater than CN2g at 64% (Fig. 1b). SLg experienced the lowest survivorship overall: 48% in the fore reef and 6% in the patch reef habitat (Fig. 1c). Fore reef site ML had the lowest survivorship of all sites (14%), apparently due to disease observed there, while the other 2 fore reef sites exhibited 83 and 79% survivorship across genotypes (Fig. S2). In the patch reef habitat, SLg and HSg genotypes showed poorer survivorship than at fore reef sites (Fig. 1b,c); CN2g survived best (86%). Mortality decreased substantially after July through November 2015 (period of 2015 bleaching; Fig. 1c).

During the survey with the most severe observed bleaching in October 2015 (Fig. S1), genotype, habitat, their interaction, and site nested in habitat were all significant factors affecting bleaching score (logistic ordinal regression; all $p < 0.001$). All genotypes showed higher bleaching scores at patch reefs than fore reefs, but some genotypes (e.g. CN1g) exhibited more severe bleaching than others (e.g. CN2g). SLg bleached most severely at all sites, with 100% of live patch reef fragments completely bleached (Fig. 2b). FR and ML reefs, the deepest sites, experienced the lowest bleaching scores.

Genotype had a significant effect on change in LAI during the 18 mo experiment ($F_{3,391} = 21.7$, $p < 0.001$; Fig. 3b), as did site ($F_{4,391} = 27.5$, $p < 0.001$; nested in habitat), but habitat and the habitat \times genotype interaction did not. CN2g exhibited significantly higher change in LAI than any other genotype (Tukey-Kramer, all $p < 0.001$), approximately double that of the lowest (SLg; Fig. 3b).

Overall, snail prevalence was generally low during this experiment ($<7\%$ averaged across sites at each survey) until December 2016 (11%), when predation became the most common cause of partial mortality as opposed to disease or bleaching. Mean snail presence over all surveys was compared among genotypes, habitats, and sites (nested in habitats), with fore reef habitats showing significantly greater snail presence than patch reefs ($F_{1,391} = 5.3$, $p = 0.022$). Sites within habitats showed significant variation ($F_{4,391} = 12.3$, $p < 0.001$). During the December 2016 survey, when the greatest number of snails were observed, patch reef sites AA, HS, and ND had 24, 12, and 4% snail prevalence, respectively, while fore reef fragments at FR, ML, and PI exhibited 5, 29, and 18% snail prevalence.

DISCUSSION

Both the genotype and outplant habitat, and in some cases reef site within habitat played major roles in fragment success over their first 2 yr, while fragment size within the range tested was less important. Although small fragments bleached less than large fragments during the summer 2014 bleaching event, survivorship was virtually identical between the sizes tested. Site, independent of habitat treatment, influenced survivorship and predation in both experiments, and LAI change in the genotype experiment. Genotype also had a strong effect on LAI change, bleaching susceptibility and resultant coral mortality. These genotype differences were exacerbated in the shallower patch reef habitats where bleaching stress was higher.

There is concern in the fields of conservation genetics and population enhancement that poorly sourced restoration material (e.g. seeds or outplanted coral genotypes) may compromise the viability of restored populations, due to loss or dilution of fine-scale local adaptation of native genotypes. If *Acropora palmata* is finely adapted to local sites or habitats, genotypes outplanted to habitats similar to reefs of origin would be expected to fare better than those placed in a novel habitat. However, this was not a consistent pattern in our results, in that CN2g, which was sourced from a fore reef type habitat, showed high survivorship, growth, and bleaching tolerance across both habitat types (i.e. apparent high-performing generalist) while the one genotype (HSg) outplanted back to its native site grew less than half as much as CN1g and CN2g at that site (mean 48 cm² vs. 94 and 142 cm², respectively). HSg also showed significantly lower survivorship than CN1g and CN2g at 2 of the 3 patch reefs (see Fig. S2 in the Supplement at www.int-res.com/articles/suppl/m592p109_supp.pdf), emphasizing the potential 'mismatch' of even robust genotypes planted back to their native environments under predicted future conditions of frequent thermal stress. SLg outplants suffered almost complete mortality at non-native patch reef sites (94%), but also demonstrated poor survivorship (48%) in fore reef habitats more similar to its origin, including PI reef, located 800 m from its site of origin. Overall, with this small sample of 4 genotypes, our results appear to better fit a pattern of generalists (both high and low performers) rather than a pattern consistent with local adaptation. Drury et al. (2017) similarly reported *A. cervicornis* generalist genotypes and higher short-term growth by outplanted *A. cervicornis* genotypes sourced from differ-

ent ('foreign') sites than by the native genotype across 8 reef sites in southeast Florida. Clearly, both the establishment of a genotype in controlled culture and its re-introduction into the wild represent strong selective events. This selection as well as potential acclimation to controlled nursery conditions may dampen the observation of local adaptation in outplanted populations.

While variable bleaching patterns are often related to distinct *Symbiodinium* types across hosts, *A. palmata* in the Florida Keys has been found to host clade A3 (*Symbiodinium 'fitti'*) almost exclusively (Thornhill et al. 2006, Baums et al. 2014). Thus, the host genotype-specific differences in bleaching susceptibility observed were likely not driven by *S. fitti* clade differences. Variation in bleaching among the 4 coral genotypes was more pronounced in patch reef habitats, and bleaching scores were lower in the fore reef habitats which were situated ~2 to 3 m deeper than patch reefs. Temperature loggers at one of the patch reef sites (North Dry Rocks, see Table S1) recorded 22 d in 2015 during which temperatures exceeded 31.2°C (bleaching threshold determined for local *A. palmata* population; Williams et al. 2017; Table 1) as opposed to only 9 d at the nearest fore reef site (FR reef, 12 km southwest of North Dry Rocks; Williams & Miller 2015). This increased exposure to high temperatures at patch reef sites, presumably caused by shallower depth of the surrounding water and being sheltered from cooler, offshore water certainly contributed to the increased bleaching severity.

Slight variation in depth at differing sites could also explain the more severe bleaching at shallower PI reef during the size experiment. Interestingly, although bleaching was significantly different between size classes at ML reef, survivorship was not. We attribute these results to the relatively low number of fully bleached fragments, as compared to the genotype experiment. Intermediate bleaching (e.g.

'paling') in *A. palmata* is less likely to lead to full colony mortality (Williams et al. 2017), and thus explains the steeper decline in survivorship in the bleached SLg fragments of the genotype experiment versus the size experiment.

After survivorship, growth is an important indicator of coral success in that it contributes to both restoration goals (i.e. structural habitat provision) and biological enhancement, whereby larger colonies should source greater numbers of both sexual and asexual propagules. Surprisingly, we found increased production in 'small' fragments compared to 'large' after 30 mo, with the mean final size of surviving small fragments exceeding that of large fragments by ~25% ($261 \pm 34 \text{ cm}^2$ LAI versus $205 \pm 34 \text{ cm}^2$). While we expected the initially greater extent of growing branch tips in large fragments to produce increased tissue, contrary results coupled with equal survivorship suggests that little is gained by the added investment of 3 to 6 mo nursery propagation needed to achieve our larger size class. These results, however, should be interpreted within the context of a single genotype and the 2014 and 2015 thermal stress events, which likely drove some mortality of both fragment size classes. In the absence of thermal stress, other sources of partial mortality (e.g. disease or predation) may more quickly compromise small fragments that possess less tissue area, in which case survivorship may show more dependence on colony size (Nugues 2002, Williams & Miller 2006).

Many previous studies concerning size-dependent survivorship and growth of transplanted *A. palmata* fragments under 'normal' thermal regimes made use of storm-generated fragments, which often exceeded the size classes of this study, and may have consisted of multiple genotypes. Lirman et al. (2000) found no relationship between initial fragment size and survivorship, although the average initial size of fragments was 651 cm^2 versus our mean 78 cm^2 . Other studies (e.g. Bruckner & Bruckner 2001, Garrison & Ward 2008, Forrester et al. 2014) have found increased survivorship with increasing original size, but again this conclusion often spans size classes larger than those of the current study. Forrester et al. (2014) reported mean LAIs of 100 versus 1000 cm^2 , whereas our fragments remained within the same order of magnitude. However, similar to our results, both Lirman et al. (2000) and Forrester et al. (2014) found variable growth results with no relation to initial fragment size.

Corallivorous snail *Coralliophila abbreviata* prevalence was particular to site as well as habitat. Similarly, though disease is far more temporally variable,

Table 1. Number of days where water temperature exceeded 31.2°C during the 2015 genotype experiment. Patch reef sites are given in **bold**, all others are fore reef. Temperature data from site 'AAA' and the size experiment were not available due to logger failure

Site	Days over 31.2°C
AAA	N/A
Horseshoe	21
North Dry Rocks	22
French	9
Molasses	7
Pickles	14

we observed a disease ‘hot spot’ at the ML reef site in the genotype experiment. Actively diseased fragments with little or no signs of bleaching were observed before the peak of bleaching and continued dying at this site even after mortality at nearshore sites stabilized following relief of thermal stress in November 2015. These observations, along with the significant influence of site in determining bleaching severity, change in LAI, and survivorship highlight the crucial importance of site selection, even within described habitat strata or across small geographic distances. Spatial patterns in disease, predation, and mortality were apparent within 6 to 12 mo, suggesting that short-term pilot studies with smaller numbers of fragments may be prudent to detect favorable (or poor) sites prior to committing large-scale outplants. We acknowledge, however, that outplanting fragments across a variety of sites and habitats should spread risk of local mortality events from temporally variable stressors (e.g. cold thermal stress, storms, etc.).

Lastly, CN2g’s increase in LAI, relative bleaching resistance, and increased survivorship suggests that in certain genotypes desirable traits may be positively correlated, though potential tradeoffs in other traits still need to be evaluated (e.g. reproductive potential, skeletal density, cold tolerance, etc.). We compare our findings to those of Ladd et al. (2017), who similarly outplanted various genotypes of nursery reared *A. cervicornis* to a reef resembling our fore reef sites. Ladd et al. (2017) reported that the 2 coral genotypes that bleached most during the summer thermal stress event actually had the greatest total linear extension, in contrast with our SLg that both grew the least and bleached the most. Ladd et al.’s (2017) genotype with the highest survivorship had significantly lower total linear extension (TLE; i.e. growth) (second lowest of 8 genotypes), similar to our CN1g’s performance, but overall our genotypes displayed a smaller disparity between performance metrics. Survivorship and net growth (measured in TLE) varied significantly with genotype identity, concurring with both our findings and those of other acroporid-based studies (Bowden-Kerby & Carne 2012, Lirman et al. 2014).

Though only 4 genotypes were tested in this study, many more are now being propagated at scale. Successful elkhorn generalist genotypes such as CN2g should be carefully leveraged in maintaining a thriving population while including as much genotypic diversity as possible to support sexual reproduction and adaptive potential. Better understanding the costs and benefits of using varying sizes, genotypes, and outplant locations of these fragments will help

improve outplanting success as we rely more on active restoration to recover *A. palmata* on reefs of the future.

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