



# Reestablishing a stepping-stone population of the threatened elkhorn coral *Acropora palmata* to aid regional recovery

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**ABSTRACT:** Recovery of the elkhorn coral *Acropora palmata* is critical to reversing coral reef ecosystem collapse in the western Atlantic, but the species is severely threatened. To gauge potential for the species' restoration in Florida, USA, we conducted an assisted migration experiment where 50 coral fragments of 5 nursery-raised genetic strains (genets) from the upper Florida Keys were moved to 5 sites across 350 km of the offshore reef. Additionally, 4 fragments from the 1 remaining colony of *A. palmata* in Dry Tortugas National Park (DRTO) were added to the 2 DRTO experimental sites to test for local adaptation. To measure coral performance, we tracked coral survival, calcification, growth, and condition from May 2018 to October 2019. All 24 corals relocated to the DRTO sites survived and calcified ~85 % faster than the fewer surviving corals transplanted to the 2 upper Keys sites. While coral survival across the entire experiment did not depend on genet, there was a weak but statistically significant genetic effect on calcification rate among the corals relocated to DRTO. The DRTO native genet was among the fastest growing genets, but it was not the fastest, suggesting a lack of local adaptation at this scale. Our results indicate that DRTO, a remote reef system inhabited by the species during the Holocene and located at the nexus of major ocean currents, may be a prime location for reestablishing *A. palmata*. Assisted migration of *A. palmata* to DRTO could restore a sexually reproducing population in <10 yr, thereby promoting the species' regional recovery.

**KEY WORDS:** Connectivity · Restoration · Ecosystem services · Holocene · Threatened species · Endangered species · Assisted migration · Genetic rescue · Assisted gene flow

## 1. INTRODUCTION

The global loss of species is perhaps the greatest challenge in addressing ecosystem collapse because it is irreversible. To prevent species loss, intervening early, before populations have lost the capacity for self-renewal (e.g. humpback whale), has generally resulted in more effective and efficient conservation outcomes than waiting until drastic interventions, such as captive breeding (e.g. northern white rhinoceros), become necessary (Snyder et al. 1996). How-

ever, the removal of single, well-understood threats such as hunting is much easier than addressing chronic or pervasive stresses (Hayward 2011). Human imprints on global climate and biogeochemical cycling have driven significant biodiversity loss on land and in the marine realm (Vitousek et al. 1997, Jones et al. 2004), and concerns about extinction now include roughly a third of all coral species (Carpenter et al. 2008). In 2006, *Acropora palmata* and *A. cervicornis* were the first corals listed as threatened under the US Endangered Species Act (NMFS-NOAA

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2006), and they were soon after identified as Critically Endangered by the IUCN (Aronson et al. 2008).

The elkhorn coral *A. palmata* is the only coral species that builds the reef crest habitat zone in the western Atlantic, and it is distinctive regarding its large size: colonies can reach >5 m in diameter and >4 m in height. Patterns of ecological and geological zonation as described in the mid-20<sup>th</sup> century (Goreau 1959, Geister 1977, Marszalek et al. 1977), characterized by uninterrupted dominance of the 2 *Acropora* species for thousands of years, no longer exist today in most places (Aronson & Precht 2001, Aronson et al. 2002, Precht et al. 2004, Wapnick et al. 2004, Toth et al. 2019). Of the 2 species, *A. palmata* is arguably the more important ecosystem engineer (Macintyre & Glynn 1976), with some exceptional locations where *A. cervicornis* built thick Holocene reefs (Macintyre et al. 1977, Aronson et al. 2002). While both species suffered dramatic population declines from a disease pandemic in the late 1970s (Gladfelter 1982, Aronson & Precht 2001), the decrease in *A. palmata* is arguably more consequential

for reef morphology. Acres of dead corals were left at the reef crest, which in places, persist today in growth position (e.g. Buck Island Reef National Monument, US Virgin Islands), possibly because of a thick rind of crustose coralline algae and secondary cementation (Adey 1975). However, most *A. palmata* skeletons have been reduced to rubble over the years from a combination of bioerosion (Glynn & Manzello 2015) and hurricanes (Woodley et al. 1981), leaving flatter, less topographically complex reefs that have become non-accreting throughout the region (Alvarez-Filip et al. 2009, Perry et al. 2015, Kuffner & Toth 2016). The results of reef degradation and flattening include loss of ecosystem services such as coastal protection from storms, food security from important fisheries, and economic returns from tourism (Costanza et al. 1997, 2014, Spalding et al. 2017, Storlazzi et al. 2019).

The Dry Tortugas coral reef ecosystem, located at a latitude of 24.4°N, is the westernmost terminus of the Florida reef tract (Fig. 1). This subtropical reef system is separated from other nearby reefs to the east by a

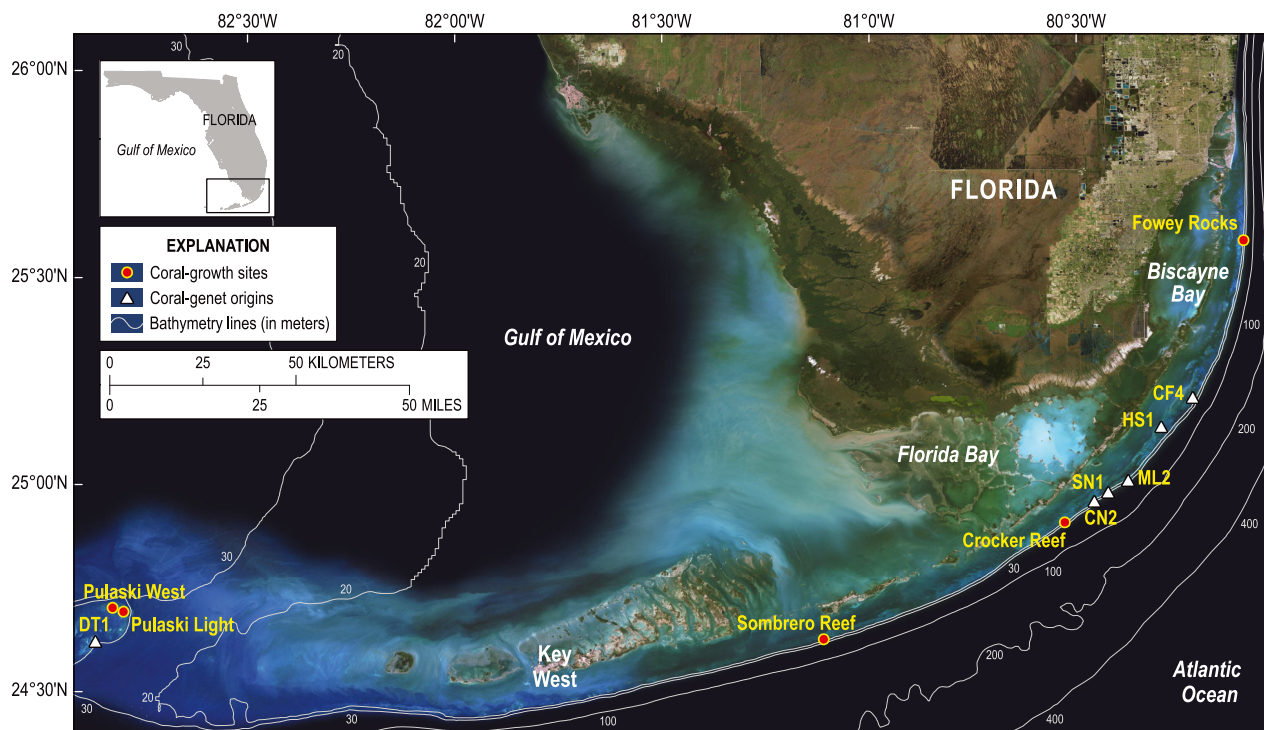


Fig. 1. Sites (white triangles) where *Acropora palmata* genets were originally harvested by the Coral Restoration Foundation (or The Nature Conservancy in Dry Tortugas) and sites (red circles) where nursery-raised fragments of those genets were transplanted to experimental blocks on the offshore reef. Experimental sites are Pulaski West (24.70°N, 82.80°W), Pulaski Shoal Light (24.69°N, 82.77°W), Sombrero Reef (24.63°N, 81.11°W), Crocker Reef (24.91°N, 80.53°W), and Fowey Rocks (25.59°N, 80.10°W). Genet collection sites are Carysfort Reef (CF), Conch Reef (CN), Dry Tortugas (DT), Horseshoe Reef (HS), Molasses Reef (ML), and Snapper Ledge (SN). Base map is uncopyrighted from World\_Imagery; source: Esri, DigitalGlobe, GeoEye, Earthstar Geographics, CNES/Airbus DS, USGDA, USGS, AES, Getmapping, Aerogrid, IGN, IGP, Swisstopo, and the GIS user community

25 m deep, 35 km wide channel, and as of this writing, it remains free of the stony coral tissue loss disease (SCTLD) that has devastated the coral communities of Florida since 2014 (Precht et al. 2016, Muller et al. 2020). The Dry Tortugas are also remote from human settlements, situated 100 km west of the nearest city of Key West, USA, and 175 km north of Havana, Cuba. Recognized early as an area of significance to human and wildlife connectivity, the US military built a fortification in the mid-1800s to defend trading routes that converge at the strategic location, the area was designated as a natural resource refuge in 1908, and the first coral reef research laboratory in the Western Hemisphere was established there in the early 1900s by the Carnegie Institute (Shinn & Jaap 2005). The shallow areas of the Dry Tortugas banks, where *A. palmata* could potentially live today, are contained within Dry Tortugas National Park (DRTO). Where reef coring investigations into the fossil record have occurred, *A. palmata* was not an extensive presence in the Holocene reefs (Shinn et al. 1977, Toth et al. 2019). However, our recent collection and dating have revealed that *A. palmata* populations were present in DRTO from ~4500 to 2700 yr BP. In historic times, Agassiz (1885) recorded living populations in areas near Garden Key, but these contracted substantially during the first half of the 20<sup>th</sup> century (Jaap & Sargent 1994), and by the 1980s, the population was confined to the existing location where only 1 patch reef persists (Davis 1982, Ruzicka et al. 2010). Genetic analysis originally suggested that the remaining DRTO population was composed of 2 genets (Baums et al. 2005), but later testing of 50 colonies in 2015 showed that only 1 remained (K. Neely, NOVA Southeastern University, pers. comm., 3 May 2020), indicating that today, the species is functionally extinct in the Dry Tortugas. Additionally, populations throughout the Florida Keys have declined precipitously, and there is little evidence of sexual recruitment of new colonies (Williams et al. 2008), necessitating the consideration of restoration interventions in the region (Miller et al. 2016).

Sitting at the nexus of several major ocean currents, the Dry Tortugas are well connected to reefs both upstream in the Caribbean and downstream in the Florida Keys. The Yucatan Current flows northward from the western Caribbean, forms the Loop Current that infiltrates north into the Gulf of Mexico, resumes eastward movement as the Florida Current, and then becomes the Gulf Stream that gains speed and flows north toward Bermuda (Lee et al. 1995). The complex hydrology of the Dry Tortugas area

results in dynamic reversals of flow speeds and directions with mesoscale eddies that cause periodic localized upwelling (Lee et al. 1995, Kourafalou et al. 2018). The ocean temperatures experienced by the shallow reefs in DRTO annually average 26.7°C, which is about 0.6°C cooler than other outer reef crest habitats to the east-northeast in the middle and upper Florida Keys reefs at similar depths (Kuffner 2020). Coral larvae are known to be transported by the Loop Current because of settlement to oil rigs throughout the northern Gulf of Mexico (Sammarco et al. 2004), suggesting that DRTO is well connected to other upstream western Atlantic reefs. Similarly, genetic data and ocean current modeling support the conclusion that DRTO's shallow reefs are well connected to the downstream reefs in the main Florida Keys; thus, there is significant potential for these reefs to be a source of coral larvae to the degraded reefs to the north (Serrano et al. 2014).

Here we report on a managed relocation experiment conducted across 350 km of the Florida reef tract to provide information relevant to the restoration of vestigial populations of *A. palmata* in the Florida Keys. Five genetically distinct individuals (genets) of *A. palmata* were sampled and sourced from the Coral Restoration Foundation (CRF, Key Largo, FL) Carysfort Reef coral nursery in the upper Florida Keys and translocated to offshore reef sites including 2 in DRTO, 2 in the Florida Keys National Marine Sanctuary (FKNMS), and 1 in Biscayne National Park (BISC). Additionally, fragments from the 1 extant colony of *A. palmata* found in DRTO were relocated to the 2 study sites within DRTO. The goal of our study was 2-pronged: (1) to test the feasibility of reestablishing a reproductive population of *A. palmata* in the Dry Tortugas by adding nursery-raised fragments from reefs in the upper Florida Keys sourced from 5 genetically distinct lineages, and (2) to compare coral growth metrics (calcification rate, height, and planar surface area) and colony condition among translocation sites and genets to explore evidence for genetic differences, environmental drivers, or interaction between genetics and environment in determining coral performance.

## 2. MATERIALS AND METHODS

### 2.1. Experimental setup

The experiment was performed at 5 US Geological Survey (USGS) calcification assessment network sites, 4 of which were previously established (Kuffner et

al. 2013, 2019) and a fifth that was added as a second site within DRTO. The second DRTO site was placed approximately 2 km west from the first and further onto the DRTO platform, in December 2016, to add spatial replication in an area that had shown exceptional coral growth in previous experiments with other coral species (Kuffner et al. 2013). The 5 sites are (from west to east) Pulaski Shoal West (PLW) and Pulaski Shoal Light (PLS) in DRTO, Sombra Key Reef Sanctuary Preservation Area (SMK) and Crocker Reef (CRK) in the FKNMS, and Fowey Rocks (FWY) in BISC (Fig. 1). Small (approximately  $5 \times 5 \times 3$  cm) *Acropora palmata* fragments of 5 genets (CF4, CN2, HS1, ML2, and SN1), with enough replicates (ramets) for placing 2 of each genet at each site, were collected by CRF staff at their Carysfort Reef coral nursery on April 24, 2018 (for main Florida Keys sites), and May 6, 2018 (for DRTO sites). The 5 genets, originally sourced from different reefs in the upper Florida Keys (Carysfort Reef [CF], Conch Reef [CN], Horseshoe Reef [HS], Molasses Reef [ML], and Snapper Ledge [SN]), were chosen by CRF based on the availability of adequate numbers of ramets in the nursery and apparent health of the donor colonies. After delivery by CRF staff, fragments were transported by vehicle in a cooler with seawater-moistened plastic bubble wrap and, upon arrival at an overnight land-based location, placed outside in coolers or buckets with seawater (freshly collected offshore) and aerated overnight. At the 2 DRTO sites, a sixth local genet was included in the experiment. Fragments of opportunity (gathered after storm breakage) from the extant DRTO colony that had been reared in The Nature Conservancy's coral nursery near Garden Key were sampled on May 8, 2018, transported by boat in seawater, and similarly kept in aerated seawater overnight. The DRTO genet was not reciprocally transplanted to the main Florida Keys sites because of logistics and permitting. Coral fragments were mounted onto plastic discs with stainless steel bolts through their centers using epoxy (All-Fix, Cir-Cut) and removably attached to cinderblocks previously installed on the reef (Fig. 2; see Morrison et al. [2013] for detailed methods and diagrams of the experimental setup).

## 2.2. Data collection

Underwater temperature data were recorded every 15 min with 2 HOBO® Water Temp Pro v2 temperature loggers (Onset®;  $\pm 0.2^\circ\text{C}$  precision)

deployed at each offshore reef site for the duration of the study (Kuffner 2020). Just before deployment and every 6 mo thereafter from spring 2018 to fall 2019, corals were removed from their blocks, transported by vessel to land, buoyantly weighed (Jokiel et al. 1978), photographed from the side and top, and measured with calipers (length  $\times$  width  $\times$  height). Calcification rates (change in dry mass per unit time) were normalized to the planar footprint area of the coral, analogous to the crown spread area of a tree's canopy (Uzoh & Ritchie 1996), at the start of each weighing interval using the caliper measurements (length  $\times$  width) and the formula for the area of an ellipse.

## 2.3. Managing risk

The risks of managed relocation of live corals (Bartz & Brett 2015, Baums et al. 2019) among the sites extending across 350 km of the Florida reef tract were considered by the authors, National Park Service, and FKNMS personnel through the scientific research permitting process and were mitigated to the maximum extent possible. We used small, single-branch fragments of coral to reduce invertebrate hitchhikers, transported the fragments on seawater-moistened plastic bubble wrap so that seawater was not transported between sites, and conducted several seawater rinses over non-reef habitat before corals were deployed to the experimental field sites. To minimize risks to DRTO natural resources, we placed our study sites at the northeasternmost corner of the park, approximately 13 km from the 1 remaining live *A. palmata* colony. *Acropora* spp. in the Caribbean are not carriers or vectors for SCTLD (Disease Advisory Committee, <https://floridadep.gov/rcp/coral/documents/are-acroporid-corals-potential-vector-stony-coral-tissue-loss-disease>), and no SCTLD has been observed in DRTO to date. Regarding the risk of genetic outbreeding depression, *A. palmata* is a well-mixed metapopulation across the western Caribbean and Florida (Baums et al. 2006), we used donor colonies from populations connected by gene flow and from environmentally similar habitats, we transplanted small fragments that were not of reproductive size, and there is only 1 extant genet in DRTO that is reproductively extinct without conspecifics with which to mate. Thus, we concluded that the risk of outbreeding depression resulting from our experiment is likely small (Baums et al. 2019).



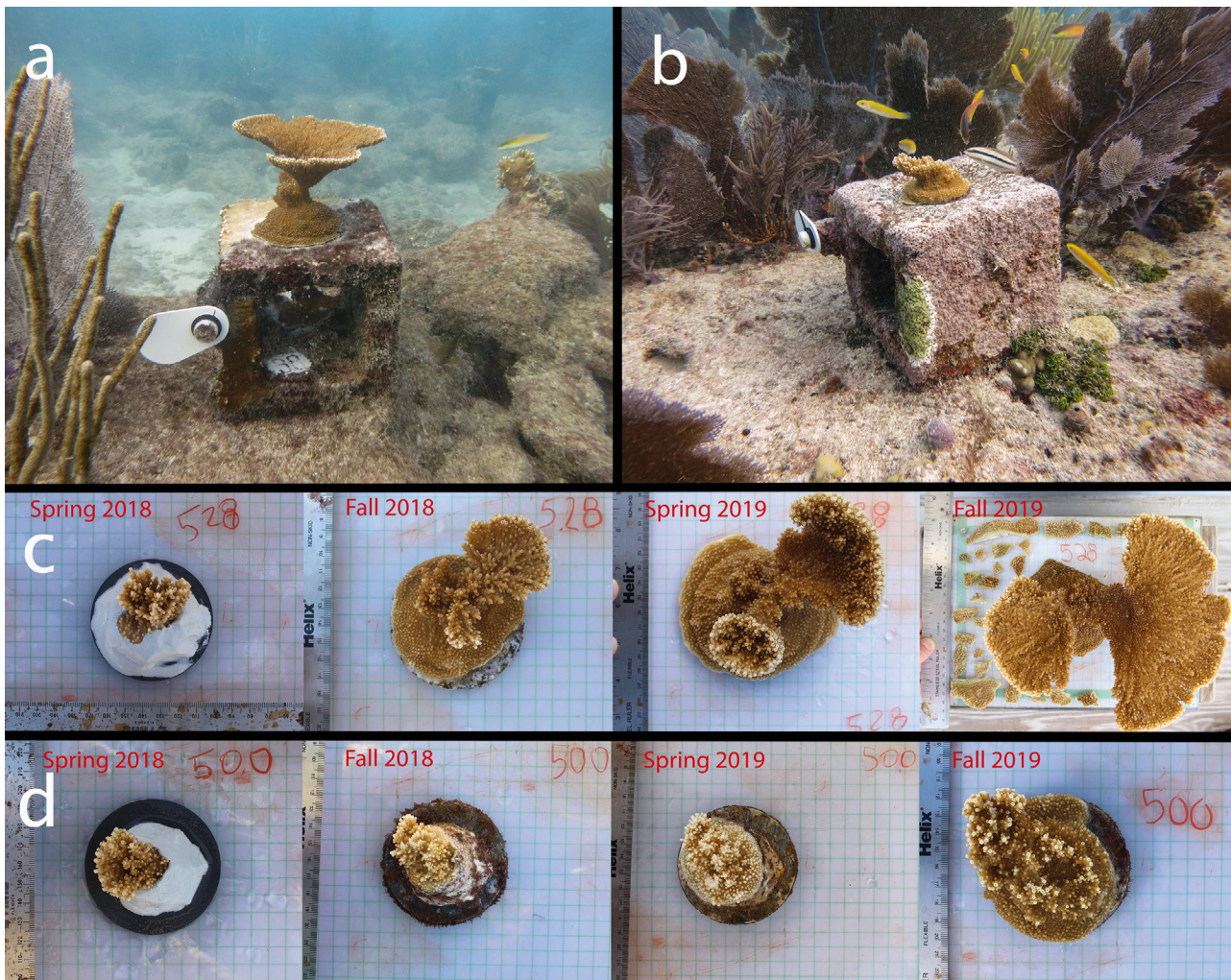


Fig. 2. Representative *Acropora palmata* colonies (both Coral Restoration Foundation genet CN2) on US Geological Survey calcification assessment network stations at (a) Pulaski Shoal Light, Dry Tortugas National Park, on November 19, 2019, coral no. 528, and (b) Crocker Reef, Florida Keys National Marine Sanctuary, on November 2, 2019, coral no. 500. (c,d) Full time series collages of the same 2 corals. The corals are epoxied to plastic discs with a stainless steel bolt protruding from the bottom so that each can be fastened with a wingnut to the permanently fixed blocks and thus removed for periodic buoyant weighing, photographing, and measuring. For scale, the cement blocks in (a) and (b) are 20 × 20 × 20 cm, and (c) and (d) have a ruler included in each image. See <https://doi.org/10.5066/P9KZEGXY> for all time-series collages (Kuffner et al. 2020)

#### 2.4. Statistics

Statistical analyses were conducted with the software package Statistix<sup>®</sup> 10.0 (Analytical Software). Chi-square tests were used to assess the effects of site and genet on coral survival rates, and a multiple comparisons test for proportions was used to test for differences among sites ( $\alpha = 0.05$ ). Two corals were removed from the chi-square tests because one was dead on arrival (at FWY) and one was lost when a block became dislodged during a storm or from anchor damage (at CRK). The Dry Tortugas genet,

DT1, was also not included because it was not transplanted to the main Florida Keys sites. To test the effects of time and site on each of the growth rate response variables, calcification rate, increase in colony height, and increase in planar footprint area, a general linear model repeated measures ANOVA was conducted, with time (3 levels) and site (5 levels) as fixed effects, the time × site interaction term included in the model, and the coral identification number as the repeated measures (random) factor. Tukey's HSD all pairwise comparisons tests were used to detect differences among sites and reported

as groupings not statistically different from each other (where different, all  $p$ -values  $< 0.05$ ). The effect of season (summer vs. winter) could not be tested because the final weighing interval (and subsequent outplanting), scheduled for April 2020, was not completed due to the COVID-19 global pandemic. In the statistical comparisons for the coral growth metrics, corals that died (defined by losing more than 50% of their live tissue) were removed from the analyses; thus, because of the mortality of genet replicates, the genetic effect was only tested among the corals deployed at the 2 DRTO sites (where survival was 100%). Two-way ANOVAs were performed on the 3 growth response variables annualized over the 18 mo experiment, with the fixed effects of site (2 levels), genet (6 levels), and site  $\times$  genet interaction term included in the models. Tukey's HSD all pairwise comparisons tests were used to detect differences among genets, and results were reported as groupings not statistically different from each other (where different, all  $p$ -values  $< 0.05$ ). To examine the relationship between increase in colony height and calcification rate, we performed simple linear regression. The distribution of temperature stress among sites and years was examined with a Friedman 2-way non-parametric ANOVA. The assumptions of homoscedasticity and normally distributed residuals were assessed and met without transformation for all variables except for planar footprint area, so those data were rank transformed. For all tests, we considered  $p$ -values  $< 0.05$  to be statistically significant.

### 3. RESULTS

#### 3.1. Survival

There was a statistically significant effect of site on *Acropora palmata* fragment survival during the study (chi-square test statistic = 22.6,  $p = 0.0002$ ), with statistically lower survival rates at FWY (3 of 9 corals) and SMK (4 of 10 corals) than at PLS and PLW, where all corals survived (Tukey's HSD,  $p < 0.05$ ). There was no genetic effect on survival across the sites (chi-square test statistic = 0.63,  $p = 0.96$ ).

#### 3.2. Calcification

The fragments transplanted to the 2 DRTO sites calcified 80 to 85% faster, averaging  $7.9 \text{ mg cm}^{-2} \text{ d}^{-1}$  ( $29 \text{ kg m}^{-2} \text{ yr}^{-1}$ ), than the fragments deployed at the 2 upper Keys sites, where calcification averaged  $4.3 \text{ mg cm}^{-2} \text{ d}^{-1}$  ( $16 \text{ kg m}^{-2} \text{ yr}^{-1}$ ); however, while survival was low at SMK, the corals that did survive calcified at levels not statistically different from those in DRTO (Figs. 2 & 3, repeated measures ANOVA, site  $F_{4,34} = 10.4$ ,  $p < 0.0001$ , time  $F_{2,68} = 1.5$ ,  $p = 0.23$ , site  $\times$  time  $F_{8,68} = 2.4$ ,  $p = 0.026$ , Tukey's HSD,  $p < 0.05$  for all pairwise comparisons, PLW and PLS  $>$  CRK and FWY). Because of fragment mortality, the genetic effect could only be tested among the corals deployed at the DRTO sites where survival was 100%, which revealed a significant effect of coral genet on calcification rate and no site effect (Fig. 3b, 2-way ANOVA on annualized data, site  $F_{1,12} = 1.7$ ,  $p = 0.22$ , genet  $F_{5,12} = 5.04$ ,  $p = 0.0102$ , site  $\times$  genotype  $F_{5,12} = 0.36$ ,  $p = 0.87$ ). Genet HS1 calcified statistically faster

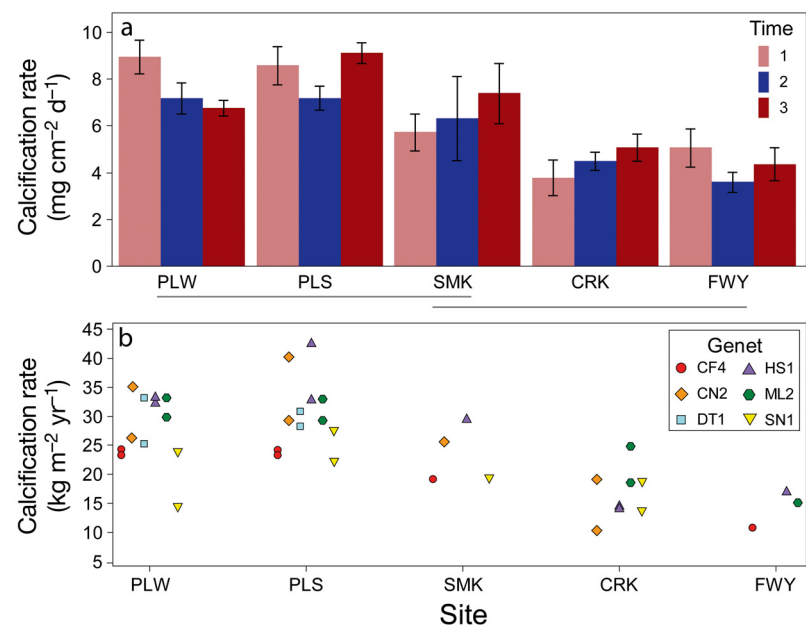


Fig. 3. Calcification rates of *Acropora palmata* colonies, normalized to planar footprint area, summarized across (a) genets for 3 sequential time intervals (time 1 = summer 2018, time 2 = winter 2019, time 3 = summer 2019) reported in  $\text{mg cm}^{-2} \text{ d}^{-1}$  with error bars  $\pm$  SE and Tukey's HSD groupings under the x-axis connecting sites not statistically different at  $p < 0.05$ , and (b) the 3 time intervals, reported in annualized calcification rates ( $\text{kg m}^{-2} \text{ yr}^{-1}$ ), for 6 different genets (see Fig. 1 for genet abbreviations) transplanted to experimental stations (Fig. 2) at 5 sites across Florida's outer reef tract. PLW: Pulaski Shoal West; PLS: Pulaski Shoal Light; SMK: Sombrero Reef; CRK: Crocker Reef; FWY: Fowey Rocks. Note that the Dry Tortugas native genet (DT1) was only transplanted to the 2 sites within Dry Tortugas National Park and was not tested at the other sites, and no data points were included in the analyses (and are not shown) for replicates that died (i.e. lost  $> 50\%$  of live tissue)



than CF4 and SN1 but equal to CN2, ML2, and DT1 (Fig. 3b, Tukey's HSD,  $p < 0.05$  for all pairwise comparisons).

### 3.3. Colony height

The rate of colony height extension was statistically higher at the 2 DRTO sites, averaging 4.8 cm yr<sup>-1</sup>, compared to rates at the 3 main Keys sites, where they averaged 1.5 cm yr<sup>-1</sup> (repeated measures ANOVA, site  $F_{4,34} = 17.7$ ,  $p < 0.0001$ , time  $F_{2,68} = 18.2$ ,  $p < 0.0001$ , site  $\times$  time  $F_{8,68} = 3.5$ ,  $p = 0.002$ , Tukey's HSD,  $p < 0.05$  for all pairwise comparisons, PLS = PLW > SMK = CRK = FWY). Height increase was also greater during the second and third time periods than during the first (Tukey's HSD,  $p < 0.05$  for all pairwise comparisons, time 1 < time 2 = time 3). The significant interaction between time and site reflects the observation that the corals in DRTO encrusted the plates during the first time period, then grew up and branched during the subsequent year, whereas the corals at the other sites were slower to completely encrust the plates and did not produce substantial branches (Fig. 2, also see time series photographs in Kuffner et al. 2020). Among the corals placed at the DRTO sites, there was also a statistically significant effect of genet on colony height extension (2-way ANOVA on annualized data, site  $F_{1,12} = 0.64$ ,  $p = 0.44$ , genet  $F_{5,12} = 6.59$ ,  $p = 0.0036$ , site  $\times$  genotype  $F_{5,12} = 1.06$ ,  $p = 0.43$ ). Genet ML2 grew taller than SN1 (Tukey's HSD,  $p < 0.05$ ). The relationship between annualized calcification rate (kg m<sup>2</sup> yr<sup>-1</sup>) and change in colony height (cm yr<sup>-1</sup>) for the 24 corals at DRTO was positive and statistically significant (simple linear regression equation:  $\Delta\text{height} = -0.0372 + 0.1655(\text{calcification rate})$ ,  $t = 4.9$ ,  $p < 0.0001$ , and  $r^2 = 0.52$ ), suggesting that measuring change in colony height (easy to measure) could be a good phenotypic growth metric for estimating coral calcification rates (difficult to measure) for this species.

### 3.4. Colony planar footprint

Corals increased the planar area they occupied faster at the 2 DRTO sites, averaging 96 cm<sup>2</sup> yr<sup>-1</sup>, than at the Florida Keys sites, where they averaged 15 cm<sup>2</sup> yr<sup>-1</sup> (repeated measures ANOVA on rank-transformed data, site  $F_{4,34} = 42.9$ ,  $p < 0.0001$ , time  $F_{2,68} = 27.1$ ,  $p < 0.0001$ , site  $\times$  time  $F_{8,68} = 0.9$ ,  $p = 0.52$ , Tukey's HSD,  $p < 0.05$  for all pairwise comparisons,

PLS = PLW > SMK = CRK = FWY). Planar footprint increase was also greater during the third time period than during the first and second (Tukey's HSD,  $p < 0.05$ , time 3 > time 1 = time 2). Within the DRTO corals, there was no significant effect of site, genet, or the interaction on change in planar footprint area of the colonies (2-way ANOVA on annualized data, site  $F_{1,12} = 0.38$ ,  $p = 0.55$ , genet  $F_{5,12} = 1.9$ ,  $p = 0.16$ , site  $\times$  genotype  $F_{5,12} = 0.46$ ,  $p = 0.80$ ).

### 3.5. Observations of stress and predation

The amount of heat stress experienced by the corals, as defined by number of days that mean daily underwater temperature exceeded the *A. palmata*-specific bleaching threshold temperature of 31.0°C (Williams et al. 2017), did not vary statistically between years or sites (Fig. 4; years: Friedman statistic = 1.8, chi-square approximation  $p = 0.18$ , sites: Friedman statistic = 5.6, chi-square approximation  $p = 0.23$ ). Notably, at Sombrero Reef during the first year, there was a spike in temperature, with 2 consecutive days over 32°C (32.4 and 32.5°C on July 17 and 18, 2018, respectively). Three corals were noted as pale during our October 2018 visit at Sombrero. The predatory snail *Coralliophila abbreviata* was observed feeding on 2 experimental colonies at FWY on May 9, 2019. Time series photographs of all corals, as well as all raw data and metadata, are published in Kuffner et al. (2020).

## 4. DISCUSSION

Our experiment demonstrated that 5 *Acropora palmata* genets sourced from the upper Florida Keys survived and flourished when transplanted to the Dry Tortugas reef system, 300 km away. Not only did all 5 genets show 100% survival at DRTO after 18 mo, 3 of the genets grew at statistically equivalent calcification rates compared to the 1 remaining extant DRTO genet, suggesting that adaptation to local-scale environmental differences (Kenkel et al. 2015) may not be a concern for this species on the scale of hundreds of kilometers across the Florida reef tract. With the successful introduction of 5 new genets, our translocation experiment has potentially supplied the remaining native DRTO genet with prospective mates, possibly rescuing it from an extreme case of the Allee effect (Knowlton 2001). If the relocated corals succeed in growing into a robust population and/or more are brought in, the

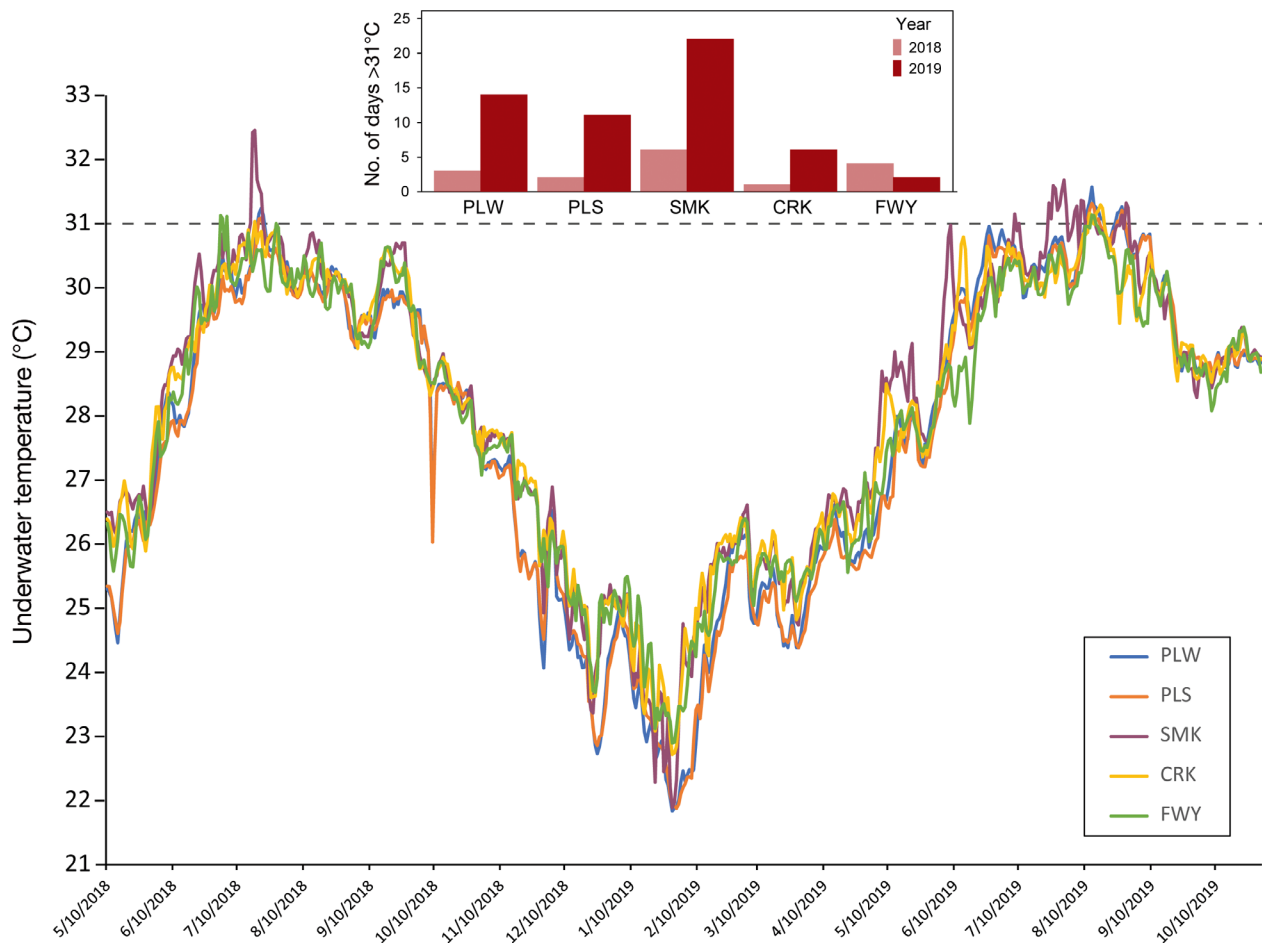


Fig. 4. Underwater temperature at the 5 experimental translocation sites (Kuffner 2020). Inset bar graph shows number of days with daily mean temperature >31.0°C (dashed gray line) in 2018 and 2019. Dates are mo/d/yr. Site abbreviations as in Fig. 3

DRTO genet, which by its persistence has proven resilient to local stresses such as cold temperature anomalies (Davis 1982) and other factors unique to its placement in the subtropical Gulf of Mexico (Jaap 2015), may contribute to future spawning events and thereby pass along any adaptive alleles that it harbors.

The same genets that flourished when moved to the Dry Tortugas did not survive or grow as well when relocated to the 2 reefs in the upper Keys closest to where the colonies were originally collected to be raised in nurseries, and it is unclear why this was so. *A. palmata* populations in the Florida Keys have continued to contract since the original white-band disease event in the 1980s (Williams et al. 2008, 2014, Miller et al. 2016), and more generally, live coral cover on offshore reefs has declined (Ruzicka et al. 2013). Several *A. palmata* reefs are in a state where only a few remnant colonies remain (Williams et al. 2008, 2014), sometimes representing a single genet

(Baums et al. 2005, 2006), indicating Allee effects and both asexual and sexual recruitment failure as likely mechanisms inhibiting population recovery (Williams et al. 2008). Our results seem to indicate that despite having originated in the upper Keys, these genets are no longer able to flourish in their natal habitat, suggesting that sexual recombination, assisted gene flow, and subsequent natural selection may be required for the species to persist in this region. The geographic significance of DRTO as an upstream site to the degraded populations in the upper Florida Keys highlights the potential value of DRTO as a source of larvae for the rest of the Keys, and genetic data from other coral species indicate widespread connectivity at this scale (Shearer et al. 2009, Serrano et al. 2014).

The management of coral reef ecosystems has for several decades been dominated by the establishment of marine protected areas, which set some restrictions on human behavior (primarily fishing) in



spaces set aside as parks or conservation refuges. This management approach has successfully increased fish biomass, abundance, and/or diversity (Jennings & Polunin 1996, Chapman & Kramer 1999, Halpern & Warner 2002, Ault et al. 2006), but evidence showing concomitant cascading effects on benthic (coral) communities has remained elusive (Toth et al. 2014, Bruno et al. 2019), as has achievement of wider socioeconomic sustainability in the absence of good governance (Sale et al. 2014). Recovery from mass coral mortality events, driven mainly by coral diseases and bleaching (Aronson & Precht 2006, Eakin et al. 2010), has not demonstrably been mitigated through marine spatial planning alone. Thus, new, more aggressive restoration and intervention methods are being considered and pursued (Hoegh-Guldberg et al. 2008, van Oppen et al. 2017). It is now recognized that nursery-raised corals may be an essential element to scaling up efforts to make measurable progress in achieving ecosystem-scale reef restoration using a wide portfolio of intervention strategies (National Academies of Sciences, Engineering, and Medicine 2019).

The importance of genetic effects on coral growth metrics was first suggested by restoration practitioners identifying certain genets as winners (growing faster and more robustly compared to others) in nursery and outplant settings. While our sample size at each site was only  $n = 2$ , our results contribute to the growing body of evidence documenting variability in growth metrics among coral genets for *A. cervicornis* (Drury et al. 2017, Kuffner et al. 2017, Lohr & Patterson 2017) and *A. palmata* (Pausch et al. 2018). Results showing that other important phenotypes vary among genets, including thermal tolerance (Kenkel et al. 2013, Lohr & Patterson 2017, Williams et al. 2017, Pausch et al. 2018) and disease resistance (Muller et al. 2018, Miller et al. 2019), are encouraging and indicate that a substantial amount of intra-species genetic variation exists upon which natural selection can act (Dixon et al. 2015, Baums et al. 2019). It might be tempting to identify and focus restoration efforts on such supercorals. However, while selective breeding experiments with genets showing promise in desirable phenotypes are important to increase our understanding of trait-based heredity and evolutionary processes, we argue that the creation of supercorals for restoration purposes could easily backfire because of phenotypic tradeoffs (Ladd et al. 2017) and because ocean conditions will continue to change rapidly and may nullify trait-based advantages (Muller et al. 2018). Thus, if selective breeding is done at the expense of collective

genetic diversity within species at restoration sites, it could have undesirable effects. It is less important to asexually propagate and preferentially outplant genets shown to be winners in today's nurseries and oceans than it is to know they exist and use them as broodstock for larval propagation aimed at maximizing recombination of genetic material (Baums et al. 2019).

Our results suggest that something about the environment in the northeastern portion of DRTO enhanced the survival and growth of *A. palmata*. Other species of coral have shown higher growth rates in the Dry Tortugas compared to the main Florida Keys, including *Siderastrea siderea* (Kuffner et al. 2013) and in our recent work on *Porites astreoides*, and there are several possible explanations for the pattern. An obvious variable relevant because of regionally increasing ocean temperatures (Kuffner et al. 2015, Manzello 2015) is simply that the *in situ* temperatures are on average about 0.6°C cooler in DRTO than at the main Florida Keys reefs; however, moderate thermal stress during our experiment was experienced across all 5 sites during both years without statistical difference among them, including at the 2 DRTO sites (Fig. 4). The strength of water flow could also be contributing to among-site differences, evidenced by the fact that diving at PLS is challenging because of strong currents and the site is ideally accessed at slack tide. However, this was not our experience at PLW, and calcification rates between these 2 DRTO sites were not statistically different (Fig. 3). Another hypothesis to test is that corals may benefit from nutritional subsidies from periodic upwelled waters containing more abundant or higher quality plankton being delivered to the shallow Dry Tortugas. Shulzitski et al. (2016), for example, showed that larval fish collected from inside high-productivity Tortugas eddies had enhanced survival and physiological condition compared to those outside eddies in the oligotrophic Florida Current. Corals that are well fed have more energy reserves and thus may be less sensitive to stressors including ocean acidification and thermal anomalies (Schoepf et al. 2013). Additionally, some coral species can up-regulate heterotrophic feeding during times of stress (Grottoli et al. 2006). However, other differences among the sites, such as in water quality variables and amount of human interaction, cannot be ruled out at this time in explaining the high growth rates we observed in the Dry Tortugas.

New subfossil evidence from reef drilling studies and surface collections on the Tortugas platform suggests that although *A. palmata* was relatively rare in

DRTO for the last 8000 yr (Toth et al. 2019), it was present for nearly 2000 yr in this area, with our samples dating from ~4500 to 2700 yr BP. The disappearance of the species generally coincides with a region-wide shutdown of reef accretion by 3000 yr BP (Toth et al. 2018). Hypothesized to have resulted from climatic cooling in the late Holocene across the region (Toth et al. 2018), this suggests that the late Holocene has been inhospitable to this cold-sensitive genus (Porter et al. 1982) at this location. With increasing ocean temperatures in the region (Kuffner et al. 2015), this location may once again support *A. palmata*, as observed for its congener, *A. cervicornis*, in southeastern Florida (Precht & Aronson 2004). *A. palmata* has also recently been observed on the high-latitude reefs of the Flower Garden Banks, where it had been absent since the relatively warm climate of ~10 000 to 7000 yr BP (Precht et al. 2014). Similarly, in the Pacific, recent expansion of several coral species has followed the northward-flowing Kuroshio Current in Japan (Yamano et al. 2011).

Our results indicate that assisted migration (i.e. reintroduction in this case) across a species' historic or Holocene range (Toth et al. 2019) can assist managers in achieving the goals outlined in species recovery plans by reducing Allee effects, increasing the potential for sexual reproduction, and thus increasing the potential for subsequent recruitment and natural selection (NMFS 2015). This may be particularly relevant to subtropical reefs, where the natural expansion of species' ranges into areas until recently too cold provides evidence that humans could assist the movement of populations as ocean conditions continue to warm at rates unprecedented during the Holocene (Marcott et al. 2013)—indeed, likely too fast for coral species to respond on their own because of decades-long generation times. However, naturally expanding populations are bringing their predators and pests with them (Yamano et al. 2011), so it behooves managers to ensure that reefs chosen for stepping-stone reintroductions are places where ecological processes, including predator–prey relationships, remain intact (Shaver & Silliman 2017, Ladd et al. 2018). Nonetheless, the Holocene record unlocks a valuable tool in coral restoration planning (Toth et al. 2019) as conditions become more like the mid-Holocene (Marcott et al. 2013) and the brief late-Holocene warm period from 1400 to 1000 yr BP (Richey et al. 2007). Since oceanic currents, seasonality, and other local-scale geophysical patterns dictated by location and ocean floor morphology are likely to be similar to those in the past, it could be very instructive to examine how species distribution

patterns varied over the past millennia in defining place-based and species-specific restoration strategies (Toth et al. 2019).

In conclusion, our findings suggest that assisted migration, guided by historic and Holocene range extensions and aimed at providing stepping-stone populations to invigorate sexual reproduction and reef connectivity, could be a useful tool in the recovery of *A. palmata* and, hence, ecosystem restoration. However, reef restoration may only be a stop-gap mechanism to help marine species persist during the time period yet to be defined by the climate change commitment (Wigley 2005), which is ever changing with continued perturbations to the global carbon cycle (Mackenzie & Lerman 2006). Depending on the climate scenario realized (Meehl et al. 2005), the ocean environment could progress quickly through and beyond the bounds of climate variability experienced during the mid- to late Holocene, potentially rendering ecosystem restoration a futile endeavor.

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