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Fine-scale environmental specialization of reef-building corals might be limiting reef recovery in the Florida Keys

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Abstract. Despite decades of monitoring global reef decline, we are still largely unable to explain patterns of reef deterioration at local scales, which precludes the development of effective management strategies. Offshore reefs of the Florida Keys, USA, experience milder temperatures and lower nutrient loads in comparison to inshore reefs yet remain considerably more degraded than nearshore patch reefs. A year-long reciprocal transplant experiment of the mustard hill coral (*Porites astreoides*) involving four source and eight transplant locations reveals that corals adapt and/or acclimatize to their local habitat on a <10-km scale. Surprisingly, transplantation to putatively similar environmental types (e.g., offshore corals moved to a novel offshore site, or along-shore transplantation) resulted in greater reductions in fitness proxies, such as coral growth, than cross-channel transplantation between inshore and offshore reefs. The only abiotic factor showing significantly greater differences between along-shore sites was daily temperature range extremes (rather than the absolute high or low temperatures reached), providing a possible explanation for this pattern. Offshore-origin corals exhibited significant growth reductions at sites with greater daily temperature ranges, which explained up to 39% of the variation in their mass gain. In contrast, daily temperature range explained at most 9% of growth variation in inshore-origin corals, suggesting that inshore corals are more tolerant of high-frequency temperature fluctuations. Finally, corals incur trade-offs when specializing to their native reef. Across reef locations the coefficient of selection against coral transplants was 0.07 ± 0.02 (mean ± SE). This selection against immigrants could hinder the ability of corals to recolonize devastated reefs, whether through assisted migration efforts or natural recruitment events, providing a unifying explanation for observed patterns of coral decline in this reef system.

Key words: acclimatization; adaptation; fitness trade-offs; inshore; offshore; Porites astreoides; *reef-building corals; selection.*

Introduction

A central problem in ecology is to understand the pattern and scale at which organisms respond to their environment (Levin 1992). This problem has received comparatively little attention in marine systems where, until recently, it was thought that most species were panmictic and unaffected by spatial and temporal variation in the environment (reviewed in Conover et al. 2006). Though it is now widely accepted that even species with planktonic larval dispersal can exhibit adaptive differentiation in response to both biotic and abiotic selection gradients, the spatial and temporal scales over which adaptation can occur remain poorly resolved (Levin 2006, Sanford and Kelly 2011).

This knowledge gap is particularly critical for reef-building corals, which constitute the foundation of the most biodiverse ecosystem in the marine environment. Coral reefs around the world have degraded significantly in recent years, particularly in the Caribbean (Gardner et al. 2003). In the Florida Keys, hard-coral communities that dominated reefs in the 1970s have now largely been replaced by soft corals, sponges, and macroalgae (Pandolfi et al. 2005; see Plate 1). The environmental factors that brought about this dramatic transition are still a matter of debate. The most widely cited causes include increasing coastal development, leading to physical damage and eutrophication (Pandolfi et al. 2005); coral disease (Aronson and Precht 2001); the 1983 epidemic that nearly wiped out Caribbean urchin populations, which are important reef herbivores (Lessios 1988); mortality from heat-induced bleaching (McWilliams et al. 2005); hurricane damage (Gardner et al. 2005); and, more recently, mortality from extreme cold events (Lirman et al. 2011).

While these factors likely contributed to the overall decline of Florida reefs, we are still largely unable to explain patterns of variation in the degree of reef deterioration at a local scale. The most prominent example of this is the contrast between inshore patch reefs and the offshore reef tract. Inshore patch reefs are characterized by increased turbidity, sedimentation, nutrients, and temperature variation (Appendix: Fig.

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A1; Lirman and Fong 2007, Boyer and Briceno 2011, Lirman et al. 2011), all of which affect coral growth detrimentally in the laboratory (Jokiel 2004, Fabricius 2005). The offshore reef tract, on the other hand, is characterized by milder temperatures (warmer in winter, cooler in summer; Fig. 1D, E) and low turbidity (Appendix: Fig. A1). Generally, one would expect that buffering by the Florida Current (a part of the Gulf Stream) and remoteness from sources of pollution on shore would facilitate better coral survival there. Contrary to this expectation, corals at inshore patch reefs in the Florida Keys consistently maintain higher cover, higher growth rates, and lower partial mortality rates than corals at offshore reefs (Causey et al. 2002, Lirman and Fong 2007).

This study tested the hypothesis that local adaptation and/or long-term acclimatization of corals to their local reef environments might be limiting reef recovery in this system. While both local adaptation and acclimatization can occur in response to different environmental pressures, adaptation is a heritable difference between populations that has evolved due to selection, while acclimatization is a plastic response that increases fitness; the response itself is not heritable, but the underlying genetic mechanisms can be (Kawecki and Ebert 2004, Pigliucci 2005, Conover et al. 2006). Given the long generation times and poorly controllable reproductive behavior of corals, it is not feasible to rear individuals and obtain an F_2 population (second filial generation offspring resulting from a cross of inshore and offshore corals) under standardized laboratory conditions in order to distinguish genetic adaptation from long-term acclimatization. Therefore, we conducted a reciprocal transplant with naturally collected *Porites astreoides* corals from four populations sourced from the Middle and Lower Keys regions to investigate the combined effects of adaptation and long-term acclimatization, which we term "specialization" (Fig. 1). Within both regions, fragments of the same coral colonies were transplanted between inshore and offshore reefs, as well as to novel sites the same distance from land as the native reefs. One sample from each coral and transplant site were taken after six months and one year to test whether native populations exhibited greater fitness in their home reef environment and to evaluate the performance of native and immigrant genotypes within a focal reef habitat (Fig. 1; Appendix: Table A1). Ultimately distinguishing between genetic adaptation and adaptive plasticity is important for developing effective management strategies (see Aitken and Whitlock 2013 for a recent review), as these mechanisms affect the rate at which coral populations and species can respond to climate change. For example, high gene flow, or population connectivity, can limit or prevent genetic adaptation to environmental conditions by swamping the effect of locally advantageous alleles. Plasticity, on the other hand, may not be impacted by high rates of gene flow among populations, if all individuals in the metapopulation possess the underlying genetic architecture necessary to produce different phenotypes in response to different environments (Pigliucci 2005). However, contemporary reef restoration methods involve transplant of naturally collected corals between reefs (Jaap et al. 2006). Therefore, the absolute response of native and foreign individuals to different environments, whether it is attributable to plasticity or genetic adaptation, is most relevant for informing current reef restoration practices.

Materials and Methods

Model coral species

Corals are cnidarians that exist in symbiosis with dinoflagellates of the genus *Symbiodinium*. This symbiosis is considered obligate, as it has been estimated that up to 95% of a coral's energy requirements are met through photosynthetically fixed carbon contributed by the endosymbiont (Muscatine 1990). Genetically variable algal symbiont types can greatly impact the capacity for coral acclimatization and adaptation to environmental variation (Little et al. 2004, Berkelmans and van Oppen 2006). Coral adaptation capacity may also be strongly dependent on the reproductive strategy of the host and the mode of symbiont transmission. *Porites astreoides* is a hermaphroditic brooding coral. Brooders release only sperm, fertilization is internal, and larvae develop within parental tissue (Richmond and Hunter 1990). These larvae are released monthly, and are competent to settle within hours, often in close proximity to their parents (Carlon and Olson 1993), resulting in highly genetically structured populations (Ayre and Hughes 2000, Underwood et al. 2007, Maier et al. 2009, Bongaerts et al. 2010). In addition, many brooders transmit their symbionts vertically from parent to offspring, again, potentially reducing gene flow. Previous work has shown highly stable host–*Symbiodinium* associations for *P. astreoides* in the Florida Keys (Thornhill et al. 2006, Kenkel et al. 2013). The choice of *P. astreoides* as a model was partly based on this potential for reduced gene flow in both host and *Symbiodinium* populations, which should facilitate local adaptation. Furthermore, this species is found in all reef environments throughout the Florida Keys and is one of the few species where populations are stable (Green et al. 2008), enabling collection of large sample sizes for robust biological replication across transplant environments.

Experimental design

Source and transplant destinations were selected based on environment "type" (e.g., reef sites displaying typical characteristics of either inshore or offshore reefs as described in the *Introduction* above), abundance of *Porites astreoides*, and feasibility of deploying and maintaining the reciprocal transplant experimental setup. For the Lower Keys transplant, 15 colonies of *Porites astreoides* were collected on 14 October 2011

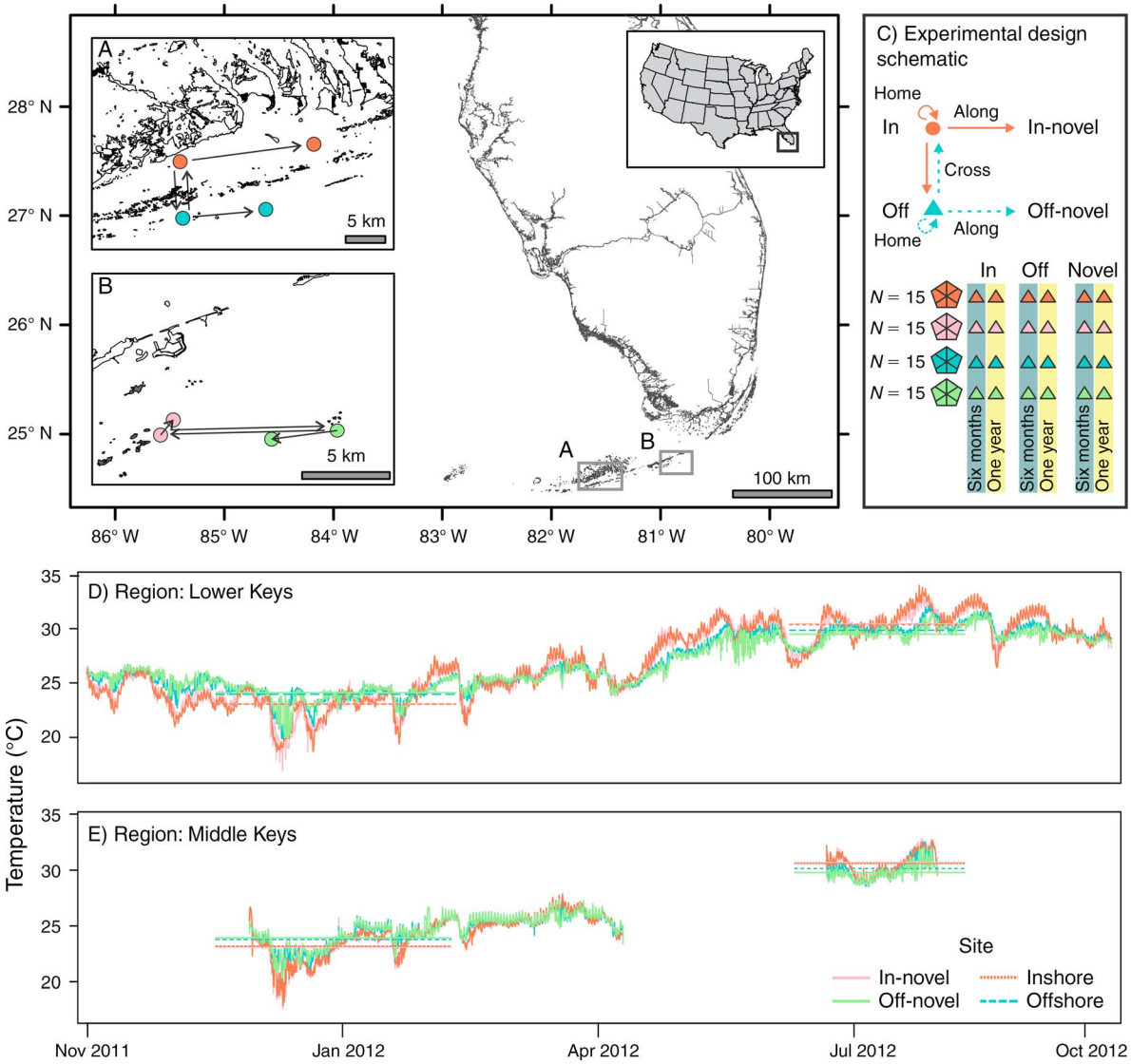

FIG. 1. Map of the Florida Keys, USA. Insets show reciprocal transplant sites for the (A) Lower and (B) Middle Keys. (C) Fifteen *Porites astreoides* corals were collected from each inshore (In) and offshore (Off) site in the Lower and Middle keys and split into six fragments. Two fragments were returned to the home site, two were transplanted cross-channel, and two were transplanted along-shore to a novel reef of the same type as the origin (In to In-novel and Off to Off-novel). One fragment of each coral from each site was collected after six months (Oct 2011–Apr 2012), and the final fragment was collected after one year (Oct 2011–Oct 2012). Benthic temperature profiles for the (D) Lower and (E) Middle Keys were obtained by in situ data loggers recording every hour. Colored horizontal lines represent the mean winter (Dec–Feb) and summer (Jun–Aug) temperatures at each reef site.

from a depth of 2–3 m from each of two sites: an inshore patch reef (Jaap Reef, 24°35.153′ N, 81°34.886′ W; Fig. 1A) and an offshore reef (Maryland Shoals Rockpiles, 24°31.299′ N, 81°34.661′ W, Fig. 1A) that are 7.2 km apart near Sugarloaf Key under Florida Keys National Marine Sanctuary (FKNMS) permit 2011-115. Corals were immediately returned to Mote Marine Tropical Research Laboratory and placed in a shaded (70% photosynthetically active radiation reducing) flow-through seawater system (raceway). On 19 October, corals were cut into six pieces using a diamond blade tile saw, and extra coral skeleton that could be removed without further damage to the live tissue was trimmed off the fragments. Coral fragments were then affixed to cement pucks using marine epoxy (All Fix Epoxy Putty, Philadelphia, Pennsylvania, USA), and each puck was labeled with a cattle tag designating both genotype (1–30) and replicate. Each puck was weighed in duplicate using a buoyant weighting method (Davies 1989). Technical replicates of mass were averaged. On 3 November, corals were reciprocally transplanted between collection sites, i.e., transplanted "cross-channel"

between inshore and offshore reefs (Fig. 1; Appendix: Table A1). In addition, corals were also moved "alongshore" to origin specific novel sites: a neighboring inshore site (Summerland Shoals Patch, 24°36.346′ N, 81°25.742′ W) for the inshore origin corals, and a neighboring offshore site (Dave's Ledge, 24°31.887′ N, 81°29.013′ W) for offshore-origin corals (Fig. 1A). Pucks were randomly assigned to cinder blocks (N = 10 pucks/block), which were cemented to the reef substrate. Blocks were cleaned of excess algal growth every 1.5 months and checked for damage and/or puck loss.

A replicate transplantation was performed in the Middle Keys. Corals were collected from a depth of 2–3 m on 18 October 2011 under FKNMS permit 2011-115 from an inshore patch reef (East Turtle Shoal, 24°43.501′ N, 80°55.120′ W) and an offshore reef (Hunt 1–4, 24°43.618′ N, 80°49.680′ W) that are 9.2 km apart near Long Key (Fig. 1B). Corals were returned to Long Key Marine Laboratory and placed in a shaded raceway. Corals were fragmented on 25 October and outplanted to the field on 31 October. Novel transplant sites were located at East East Turtle Shoal (24°43.969′ N, 80°54.738′ W) for the inshore origin corals, and Eleven-foot Mound (24°43.371′ N, 80°51.700′ W) for offshore origin corals (Fig. 1B).

In April 2012, one fragment of each coral genotype was collected from each site to represent the "six-month" time point (Fig. 1; Appendix: Table A1). Collections occurred on 24 April in the Lower Keys and 27 April in the Middle Keys. The final fragments were collected in October 2012, representing the "one-year" time point (Fig. 1; Appendix: Table A1). Collections occurred on 3 October in the Lower Keys and 5 October in the Middle Keys. Pucks were cleaned of algal growth and again buoyant weighted in duplicate. Coral fragments were then removed from their pucks and frozen on dry ice. Fragments were kept at −80°C, shipped to The University of Texas at Austin on dry ice and again stored at −80°C until processing.

Environmental disturbances, including Hurricane Issac in August 2012, resulted in the stochastic loss of some coral fragments at each site (Appendix: Table A1). All fragments were recovered in the Lower Keys following six months. After one year, two fragments were lost from inshore sites, and seven from offshore sites in the Lower Keys. In the Middle Keys, four fragments were lost from inshore reefs and 17 from offshore reefs following six months. After one year, 17 fragments were lost from inshore reefs and 22 from offshore reefs in the Middle Keys.

Environmental data

Data loggers (measurement accuracy: ±0.53°C, HOBO Pendant Temperature/Light Data Logger, Onset, Bourne, Massachusetts, USA) recorded temperatures at each of the transplant sites every hour. Additional water quality data for the Florida Keys were sourced from the Southeast Environmental Research Center, Florida International University (SERC-FIU) Water Quality Monitoring Project for the Water Quality Protection Program of the Florida Keys National Marine Sanctuary, which is supported by EPA Agreement number X994621-94-0 and NOAA Agreement number NA09NOS4260253. SERC-FIU maintains a publicly available data set of water quality data, collected quarterly from 1995 to the present, for a network of 112 sites spaced throughout the Florida Keys National Marine Sanctuary. The sites are classified into general reef regions (Lower, Middle, Upper Keys, et cetera) and defined by reef location (inshore, offshore, channel, et cetera). While reciprocal transplant sites used for this study are within the general water quality survey regions, these sites are not identical to those repeatedly monitored for water quality by SERC-FIU. Therefore, to evaluate potential impacts of water quality on coral growth, water quality data from the Lower Florida Keys was extracted from the SERC-FIU data set to create two series of nonoverlapping four-site groups (N = 4 four-site groups per series) replicating the transplant design as shown in Fig. 1C: an inshore (In)–offshore (Off) site pair with two "along-shore" flanking sites (inshore to inshore and offshore to offshore). Series A corresponds to the following sets of monitoring stations, listed in order of "In," "Off," "In-novel," "Off-novel": (274, 276, 271, 273); (268, 270, 266, 267); (260, 263, 257, 259); (254, 256, 250, 252), while series B corresponds to (277, 279, 274, 276); (271, 273, 268, 270); (266, 267, 260, 263); (257, 259, 254, 256) (locations *available online*).[2]

Phenotypic trait measurements

Percentage of mass gain, total protein, total carbohydrate, total lipid, *Symbiodinium* density, chlorophyll *a*, and chlorophyll c_2 content were quantified in all recovered coral fragments at the six-month and one-year time point. Tissue growth largely occurred at fragment margins, over the original cut lines (Appendix: Fig. A2), and was therefore not proportional to the initial live surface area. Coral growth was assessed by calculating the percentage of mass gained by each coral fragment based on buoyant mass of the fragment before and after the experiment, measured as described in Kenkel et al. (2013). There was no tendency for the percentage of mass gain to depend on the initial size of the fragment (Appendix: Fig. A3). Coral tissue surface area was quantified at the end of the experiment using the aluminum foil method (Marsh 1970), and this surface area was used to standardize additional physiological trait measures. Surface areas of recovered fragments were 7.2 ± 1.6 cm^2 (mean ± SE) in size, on average.

To evaluate physiological condition of the coral, tissue was removed from the frozen samples using an

[2] http://serc.fiu.edu/wqmnetwork/FKNMS-CD/lowkeys.htm

airbrush with extraction buffer (50 mM phosphate buffer, pH 7.8, with 0.05 mM dithiothreitol) over ice (Palmer et al. 2010). Tissue slurries were homogenized by vortexing with 1-mm glass beads (BioSpec, Bartlesville, Oklahoma, USA) for 1 min and left on ice for 5 min, after which, 1 mL of this slurry was aliquoted for symbiont density analysis. *Symbiodinium* cell numbers were determined by conducting four replicate counts of 10-μL samples using a haemocytometer and a compound microscope (100× magnification). Densities were expressed as the number of symbiont cells per cm^2 of coral surface area.

The remaining slurry was centrifuged at 4°C at ~24 157 m/s^2 (3500 rpm) for 5 min to separate coral and endosymbiotic algal fractions. Photosynthetic pigments were extracted from the algal pellet by 24 hr incubation in 90% acetone at 4°C. Chlorophyll content (a and c_2) was assessed by triplicate measures of pigment extract absorbance at 663 nm and 630 nm on a Spectramax M2 spectrophotometer (Molecular Devices, Sunnyvale, California, USA). Pigment content was quantified using the equations described in (Jeffrey and Haxo 1968) and expressed as ng of pigment per cm^2 of coral surface area.

The supernatant was aliquoted for host protein, carbohydrate, and lipid analysis and frozen at −20°C (1 mL each). Total protein was extracted by incubating the protein aliquot 1:1 in 0.2 mol/L NaOH for one hour at 90°C. This extract was centrifuged at ~24 157 m/s^2 (3500 rpm) for 5 min to separate cell debris from the solution and 20 μL clear supernatant was assayed in triplicate using a Pierce BCA assay kit following the manufacturer's instructions (Fisher ThermoScientific, Waltham, Massachusetts, USA). Blank 0.1 mol/L NaOH samples and BSA protein standards (0.125, 0.25, 0.5, 0.75, 1, 1.5, and 2 mg/mL) were run in triplicate on each plate and absorbance was read at 562 nm on a Spectramax M2 spectrophotometer. Standard curves had an R^2 of 0.96–0.99. Total protein content per sample was expressed per cm^2 of coral surface area. Carbohydrate was quantified using a phenol-sulfuric acid method following the protocol described in Masuko et al. (2005). Blank samples and D-Glucose standards (0.03125, 0.125, 0.25, 0.5, 1, and 2 mg/mL) were run in triplicate on each plate and absorbance was read at 485 nm on a Spectramax M2 spectrophotometer. Standard curves had an R^2 of 0.90–0.99. Total carbohydrate content per sample was expressed per cm^2 of coral surface area. Total lipid extractions were completed for a subset of samples (Lower Keys, one-year cross-channel samples only) by Boston University's School of Medicine Core Facility. For each sample, 400 μL of the host tissue aliquot was extracted with 8 mL chloroform (2) : methanol (1) and 1.6 mL acid saline. The lower phase was removed, dried under nitrogen, and resuspended in 0.5 mL chloroform : methanol. Two 25-μL aliquots were dried and weighed, and the average was used to calculate total lipid in μg/mL. Total lipid content per sample was expressed per cm^2 of coral surface area.

Statistical analyses

Selection against transplants at each reef site was calculated as in Hereford (2009); for example:

$$s_{\text{inshore}} = \frac{W_{\text{native inshore pop at inshore reef}} - W_{\text{transplanted offshore pop at inshore reef}}}{\bar{W}_{\text{all corals at inshore reef}}}$$

using the percentage of mass gain as a proxy of fitness (W), and these selection coefficients were averaged across sites. We used mass gain as a fitness proxy because reproductive capacity in *P. astreoides* is positively correlated with colony size; therefore, increases in size indicate greater potential fecundity (Chornesky and Peters 1987). The magnitude of fitness trade-offs, as quantified by the percentage of mass gain, was calculated as in (Bennett and Lenski 2007) and it describes the correlation between the fitness advantage of a focal population at its native reef site (relative fitness in the native environment, i.e., "home") and the fitness advantage of the population at a nonnative site (relative fitness in the nonnative environment, i.e., "cross-channel" and "along-shore"). Relative fitness in the native environment is calculated as in the equation given above. For calculating relative fitness in the nonnative environment, we used, for example, the following equation:

$$s_{\text{inshore}} = \frac{W_{\text{transplanted inshore pop at offshore reef}} - W_{\text{native offshore pop at offshore reef}}}{\bar{W}_{\text{all corals at offshore reef}}}.$$

All analyses were carried out using R 2.15.3 (R Development Core Team 2013). Differences in absolute trait values (percentage of mass gain, symbiont density, total protein, total lipid, total carbohydrate, chlorophyll a, and chlorophyll c_2) were evaluated with respect to time of sampling (six months and one year), region (Lower and Middle Keys), reef origin (inshore and offshore) and transplant destination (home, cross-channel, and along-shore) using a nested series of linear mixed models implemented in the nlme package (Pinheiro et al. 2013). Symbiont cell density was square root-transformed and total chlorophyll (a and c_2) were log-transformed prior to statistical analyses. For all models, time, region, origin, transplant, and trait measurements were modeled as fixed factors. Colony identity was included as a scalar random factor. Model selection was performed using Akaike information criterion (AIC), using the *stepAIC* command from the *MASS* package (Venables and Ripley 2002) to step through all nested models in both directions (from single factors to inclusion of all interaction terms and vice versa). We required a delta AIC (Δ_{AIC}) of at least two to justify selection of a top model. Wald tests were used to evaluate significance of individual predictors (fixed factors and interactions) within the top model. For

PLATE 1. Coral reef in the Lower Florida Keys (USA). Photo credit: Michael Sweet, the University of Derby.

percentage of mass gain data, nominal P values for the significance of pairwise differences between levels of fixed factors were derived via Markov chain Monte Carlo (MCMC) simulations using the package *MCMCglmm* (Hadfield 2010). For physiological trait models, Tukey's HSD test was used to evaluate significance of pairwise difference between specific transplant destinations (i.e., home, cross-channel, and along-shore) when the factor "transplant destination" was deemed significant overall by the Wald test. We also explored the relationship between the primary fitness proxy, percentage of mass gain, and other physiological trait measurements in a separate series of linear mixed models. Each trait (protein, carbohydrate, lipid, *Symbiodinium* density, chlorophyll *a*, and chlorophyll c_2) was independently modeled as a fixed factor, and colony identity was included as a scalar random factor. In this case, model selection was performed using the *AICcmodavg* package (Mazerolle 2013) to compare models using the same AIC criteria described above.

To evaluate the potential impacts of water quality and temperature metrics on coral growth, we calculated the absolute value of the difference in 16 water quality parameters between each site pair (inshore to inshore, inshore to offshore, and offshore to offshore) at each sampling time point, generated as described above in *Materials and methods: Environmental data*. In situ logger data was used to calculate differences in water temperature between actual transplant sites at each hour sampling interval for the Lower and Middle Keys transplant sites. In addition to mean temperature, we also quantified variation in time spent at extreme temperatures (proportion of time below 22°C in winter and above 31°C in summer) and magnitude of high-frequency temperature fluctuations assessed as the 90% quantile of the daily temperature range (i.e., the largest daily temperature range observed once every 10 days). A nonparametric Mann-Whitney rank sum test was used to compare among-site differences for each water quality parameter. Significance was recorded when both replicate site series exhibited $P < 0.05$ for a particular type of contrast (i.e., inshore-offshore, along-inshore, or along-offshore). For promising environmental variables, we then used a linear mixed model to better evaluate their effect, modeling the candidate variables and coral origin as fixed factors and including colony identify as a scalar random factor. A Wald test was again used to evaluate the significance of factors and interaction terms.

RESULTS

Local specialization patterns: "home vs. away"

Physiological changes in response to transplantation were complex and were best explained by models with

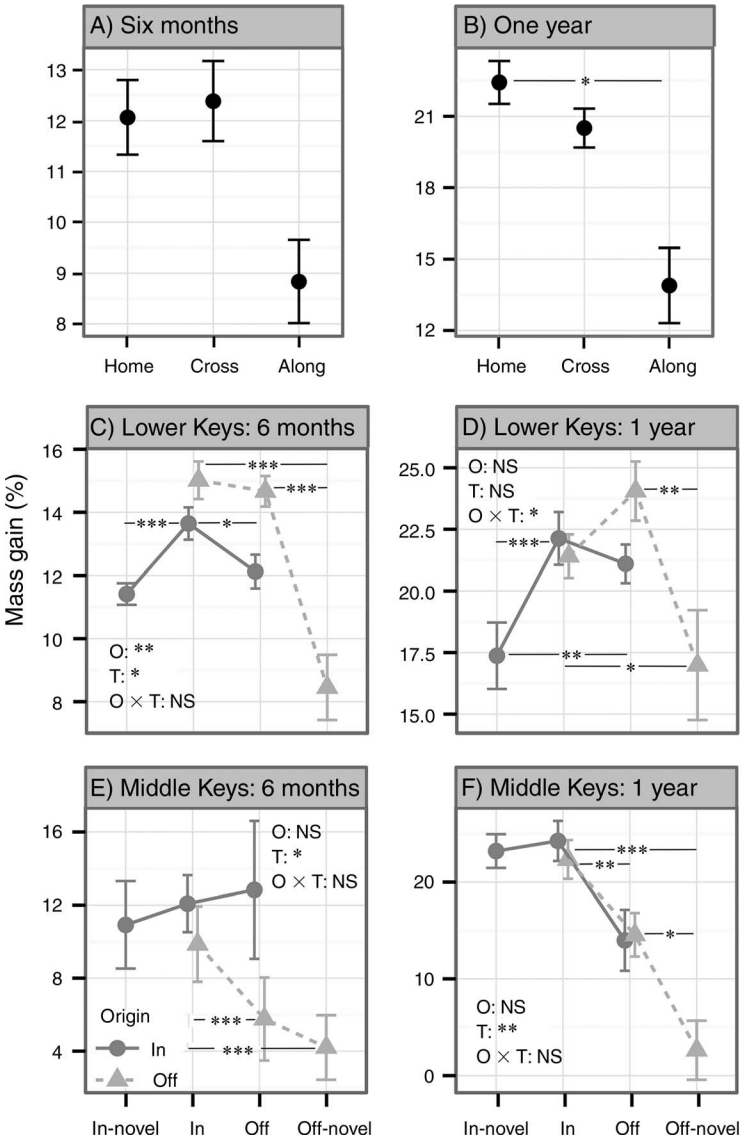

FIG. 2. Percentage of mass gain (mean ± SEM) in source coral populations when transplanted to different habitats in the Florida Keys. Average mass gain for all populations by transplant destination following (A) six months and (B) one year. Lower Keys populations after (C) six months ($N = 90$) and (D) one year of transplant ($N = 81$); and Middle Keys populations after (E) six months ($N = 69$) and (F) one year ($N = 51$). Abbreviations are: O, effect of population origin; T, effect of transplant destination; and O × T, effect of the origin by transplant interaction. See Fig. 1 for a diagram of the experimental design. Significance of post hoc pairwise comparisons between transplant destinations for corals originating from the same reef: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$; NS, not significant.

multiple higher-order interaction terms (Appendix: Fig. A4, Tables A2–A8). However, Wald tests for individual terms within these models revealed some generalities. Percentage of mass gain and host physiological trait values were highest at the home reef following one year of transplantation, consistent with the hypothesis of local specialization (Figs. 2B, D, F, and 3A–C). Furthermore, transplantation along-shore to novel sites within the same environmental type (Figs. 1–3) resulted in the greatest reductions in mass gain and host traits of total protein and total carbohydrate, contrary to our initial expectations that the greatest detrimental effect would be observed in the cross-channel transplantation. We first focus on the results for percentage of mass gain, as this trait most closely reflects coral fitness.

Percentage of mass gain was significantly impacted by transplant destination ($P_{\mathrm{WALD}} < 0.0001$) and the destination by sampling time point interaction ($P_{\mathrm{WALD}} < 0.05$; Fig. 2; Appendix: Table A2). Following transplantation along-shore, mass gain was reduced by 3.1% after six months ($P_{\mathrm{MCMC}} = \mathrm{NS}$) and 8.2% after one year ($P_{\mathrm{MCMC}} < 0.05$) in comparison to mass gained by

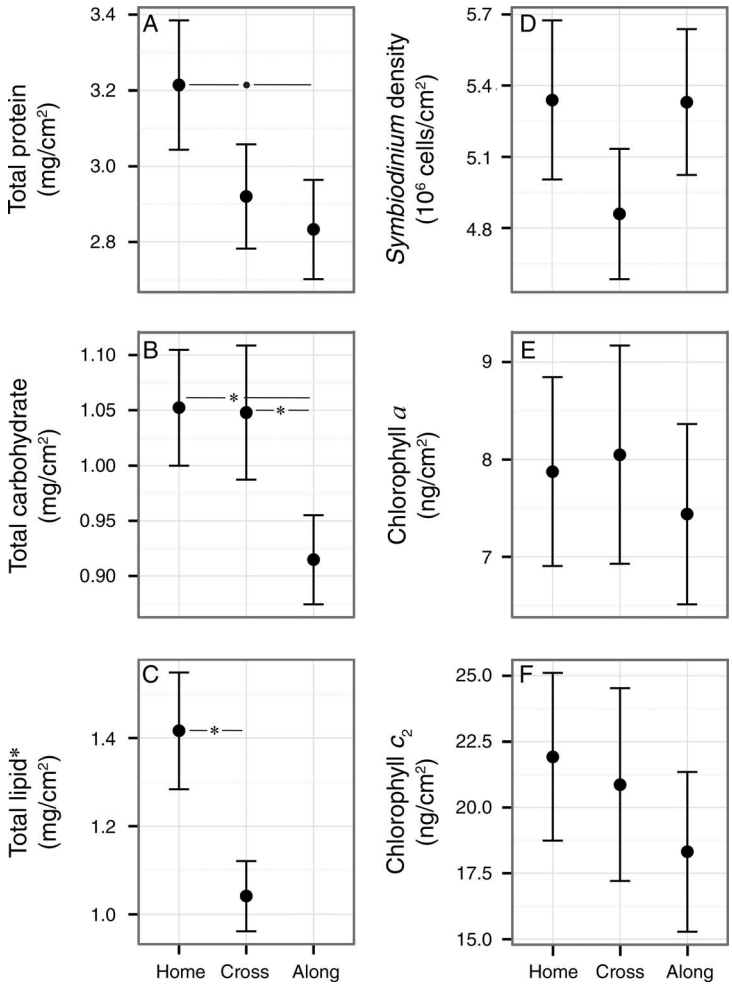

FIG. 3. Phenotypic differences (mean ± SEM) in coral physiological traits with respect to transplant destination, averaged over both sampling time points: (A) total protein of the coral host, (B) total carbohydrate of the coral host, (C) total lipid of the coral host, (D) *Symbiodinium* density, (E) chlorophyll *a*, and (F) chlorophyll c_2. Total lipid content was only analyzed for coral fragments from the Lower Florida Keys at the one-year time point. Significance of post hoc pairwise comparisons: $P < 0.1$, * $P < 0.05$.

corals at the home reef site (Fig. 2A, B). Cross-channel transplantation did not decrease mass gain of corals during the first six months, but resulted in a 1.6% reduction on average following one year ($P_{\mathrm{MCMC}} = \mathrm{NS}$; Fig. 2A, B). While inshore-origin corals exhibited higher mass gain, on average, in comparison to offshore origin corals (estimated effect size, $\beta = 3\% \pm 1.2\%$ [mean ± SE], $P_{\mathrm{WALD}} < 0.01$; Fig. 2; Appendix: Table A2), inshore-origin corals were more affected by the cross-channel transplant than offshore origin corals ($P_{\mathrm{WALD}} < 0.0001$; Fig. 2; Appendix: Table A2).

In the Lower Keys, inshore-origin corals showed growth trends consistent with local specialization after only six months: Growth was reduced in both nonnative environments in comparison to growth at the home reef ($P_{\mathrm{MCMC}} < 0.05$; Fig. 2C). While offshore-origin corals showed a significant effect of along-shore transplantation at this time point ($P_{\mathrm{MCMC}} < 0.001$), they appear unaffected by the cross-channel environment, exhibiting mass gains similar to their native reef counterparts (Fig. 2C). In Middle Keys corals, this pattern was reversed. Inshore-origin corals were unaffected by transplantation, while offshore origin corals showed a pattern of local maladaptation: Offshore-origin corals increased mass gain in the cross-channel environment, though growth is still suppressed along-shore following one year of transplantation (Fig. 2E).

Significant differences with respect to origin and transplant destination were observed after one year ($P_{\mathrm{WALD}} < 0.05$; Figs. 1D, E and 2D, F; Appendix: Table A2). In the Lower Keys, the trends observed after six months were largely preserved; however, offshore origin corals no longer outgrow natives at the inshore reef, leading to a significant origin by treatment interaction ($P_{\mathrm{MCMC}} < 0.05$; Fig. 2D). As a result, in the Lower Keys after one year, mass gain was

highest at the native reef for both inshore and offshore origin corals. In the Middle Keys, the six-month patterns were also mostly retained, save for the response of inshore corals at the offshore site, which demonstrated suppressed growth at the offshore location. After one year, this population was the only one to exhibit mass gain patterns consistent with initial predictions: Inshore corals were unaffected by transplantation to a novel inshore reef site, but exhibited a significant disadvantage at the offshore reef ($P_{\mathrm{MCMC}} < 0.01$; Fig. 2F).

Additional physiological traits in the coral host also exhibited patterns that indicate better performance at the home reef site. The overall effects of transplant destination on total coral protein and carbohydrate content were marginally significant ($P_{\mathrm{WALD}} = 0.055$ and 0.066, respectively; Fig. 3A, B; Appendix: Tables A3 and A4). Total protein content was reduced by 0.29 mg/cm^2 in the cross-channel transplants and 0.38 mg/cm^2 in the along-shore transplants relative to their home reef counterparts (Fig. 3A). Given that the total measured protein content in recovered coral fragments was ~3 mg/cm^2 (Fig. 3A), this decrease corresponds to the loss of about 10% of total protein. Total carbohydrate content was not affected by the cross-channel transplant, but decreased by 0.14 mg/cm^2 in along-shore transplants relative to the home reef transplants (Fig. 3B). Total lipid was only analyzed in corals from the Lower Keys following one year of transplantation cross-channel. There, lipid content was 0.38 mg/cm^2 higher in corals at their native reef site ($P_{\mathrm{WALD}} < 0.05$; Fig. 3C; Appendix: Table A5), again consistent with local specialization. Symbiont-related traits of total cell density, chlorophyll *a*, and chlorophyll c_2 content were not significantly affected by transplant destination (Fig. 3D–F; Appendix: Tables A6–A8).

Regression analyses exploring the relationship between the percentage of mass gain and additional phenotypic trait data revealed weak, though positive, linear relationships (Appendix: Fig. A5). However, only models that incorporated symbiont density and total protein showed $\mathrm{AIC_c}$ values that indicated an improvement over the null model (Appendix: Table A9). These traits were significantly positively correlated with growth, though the overall variance explained by these measures was low, only 10% and 2% for total protein and *Symbiodinium* density, respectively (Appendix: Fig. A5A, B).

Investigation of putative selective agents structuring coral populations along-shore

Given the substantial fitness impacts of along-shore transplantation on coral growth and energetic status (Figs. 2 and 3), a post hoc analysis of water quality was conducted to evaluate variation among along-shore sites relative to cross-channel differences using a publicly available data set from fixed monitoring stations in the Lower Florida Keys (SERC; *available online*).[3] In addition, we calculated temperature metrics from in situ loggers: mean temperature, the proportion of time spent above 31°C and below 22°C, and the 90% quantile of the daily temperature range (90%DR), which can be understood as the largest daily range observed once every 10 days, on average.

We hypothesized that environmental variables showing greater variation among along-shore site pairs relative to cross-channel pairs would be the most likely candidate selective agents impacting coral fitness in along-shore transplants. However, of 16 water quality variables sourced from SERC, none showed significantly greater variation at along-shore sites (inshore to inshore or offshore to offshore) relative to the inshore-offshore comparison (Fig. 4A–P). For temperature metrics, mean temperature and threshold temperatures showed a pattern similar to the water quality data: variation was greatest among cross-channel site pairs (Fig. 4Q–S) and none of these metrics explained a significant proportion of the variation in coral mass gain (Appendix: Fig. A6). The 90%DR, however, showed a pattern consistent with our hypothesis: Neighboring along-shore sites were more different from each other than cross-channel site pairs in six out of eight comparisons (Figs. 4T and 5A, B).

A subsequent linear model revealed that the 90%DR had a significant negative effect on coral growth at both sampling time points ($P_{\mathrm{WALD}} < 0.0001$; Fig. 5C, D), but this effect also depended on the coral origin ($P_{\mathrm{WALD}} < 0.05$). For offshore origin corals, the 90%DR explained 27% of the variation in growth following six months and 39% of the variation in growth after one year, with a 12–19% decrease in the percentage of mass gain per degree increase in the 90%DR (Fig. 5C, D). In contrast, there was no correlation between the percentage of mass gain and 90%DR in inshore-origin corals at the six-month time point (Fig. 5C). At the one-year time point, the 90%DR explained only 9% of the variation in growth among inshore-origin corals, with a 9% decrease in the percentage of mass gain per degree increase in the 90%DR (Fig. 5D).

Strength of selection against transplants: "local vs. foreign"

The strength of selection against transplants can be defined as the difference in relative fitness between a native and nonnative population in the native population's environment (Hereford 2009). Using percentage of mass gain as a proxy of fitness, the overall strength of selection after one year of transplantation was 0.07 ± 0.02 (mean ± SE), as foreign corals demonstrated, on average, 7% less yearly growth than native corals (Table 1). This measure also reflects the magnitude of local specialization of a given population. While corals in the

[3] http://serc.fiu.edu/wqmnetwork/FKNMS-CD/index.htm

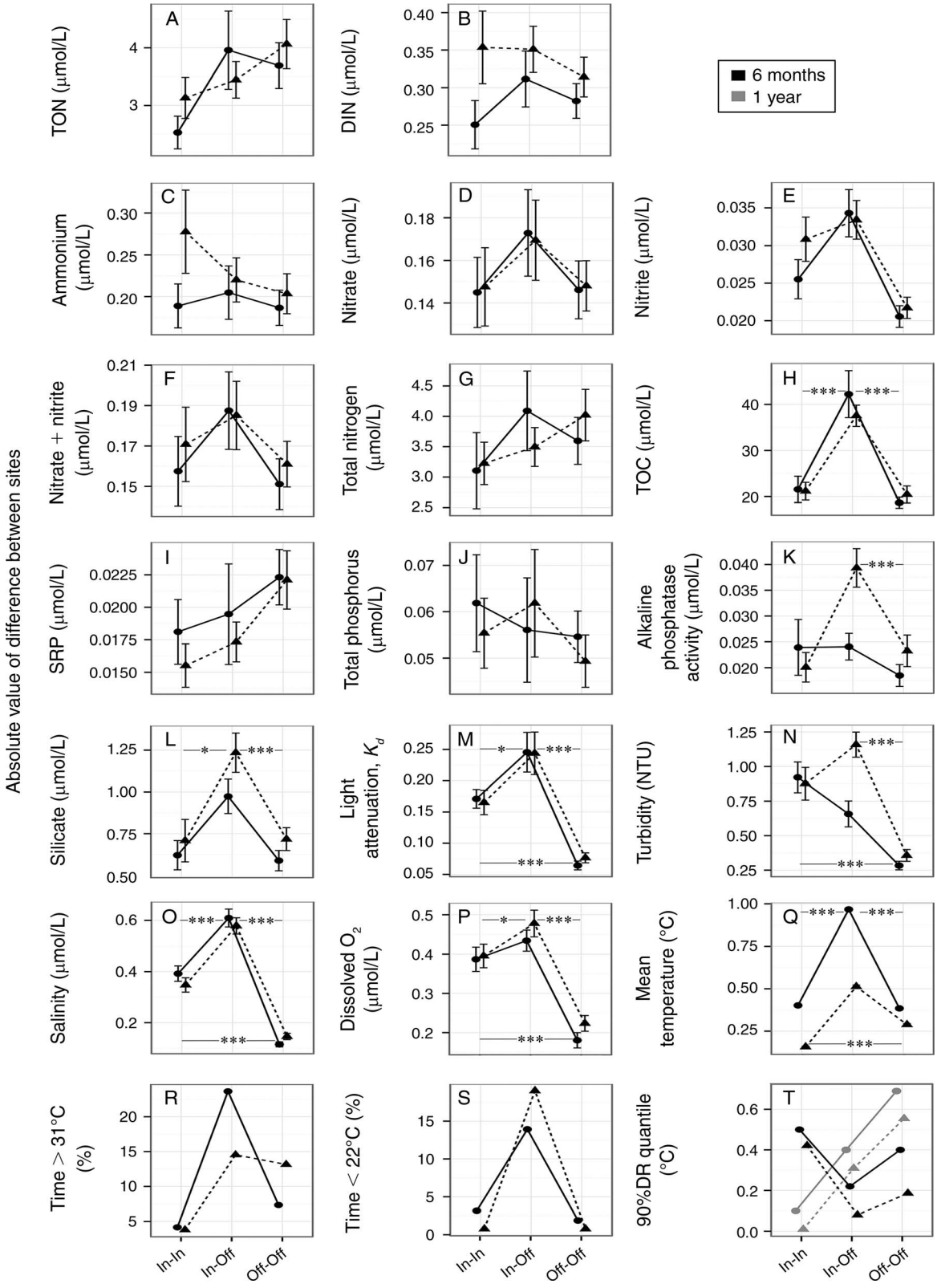

FIG. 4. Differences in abiotic environmental parameters between reef type destinations. Mean ± SEM for the absolute value of the difference in each water quality metric between neighboring inshore sites (In-in), cross-channel sites (In-off), and offshore sites (Off-off). In panels A–P, symbols correspond to two independent replicate series of four-site pairs ($N = 4$ four-site pairs per series)

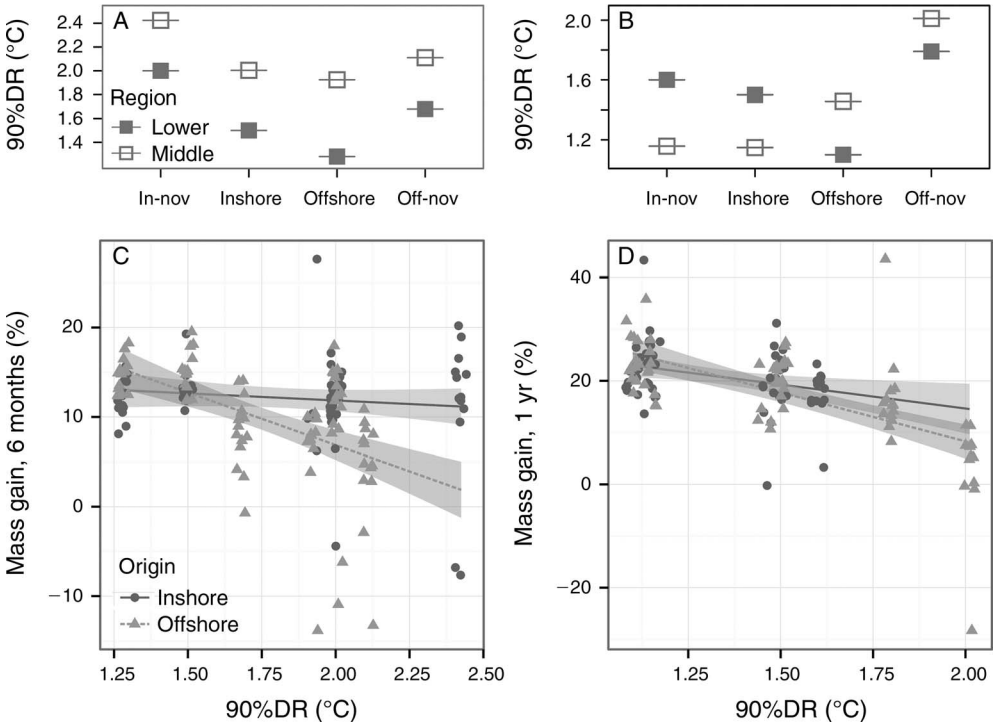

FIG. 5. The 90% quantile of the daily range in temperature (90%DR) at a reef site explains a significant proportion of the variation in the percentage of mass gain. The 90%DR by reef site after (A) six months and (B) one year. The percentage of mass gain in corals from inshore and offshore reefs as a function of the 90%DR following (C) six months and (D) one year of transplantation. The shaded area around the regression lines indicates the 95% confidence interval.

Lower Keys displayed a significant origin by transplant interaction after one year, consistent with local specialization, it must be noted that transplant destination had the most effect on corals in the Middle Keys ($P_{MCMC} < 0.01$; Fig. 2F). This conclusion is also contingent on the time of sampling. After six months, two of the four native populations exhibited lower fitness than that of foreign transplants: inshore corals from the Lower Keys ($P_{MCMC} < 0.01$; Fig. 2C) and offshore corals from the Middle Keys ($P_{MCMC} =$ NS; Fig. 2E).

Costs of local specialization

Maximization of mass gain in the native environment incurs a trade-off in the ability of corals to grow in a foreign environment. Population-level trade-offs, defined as pairwise comparisons between populations grown in each other's native environments, showed a temporal effect. All fully reciprocal population pairs (i.e., cross-channel transplants) exhibited greater relative fitness in their native environment, but only after one year of transplantation (Fig. 6). No trade-offs are evident at the six-month time point.

DISCUSSION

Evidence of local specialization

Two criteria are generally used to test for local specialization: "home vs. away," which considers the performance of a given genotype "at home" and "away," and "local vs. foreign," which considers the performance of "local" and "immigrant" genotypes within each test habitat (Kawecki and Ebert 2004). Though the results of this experiment were complex (Appendix: Fig. A4), after one year of transplantation corals exhibited the greatest mass gain, had significantly higher levels of total lipid, and exhibited marginally significant increases in protein and carbohydrate content in their home reef environment, satisfying the "home vs.

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simulating the transplant design as shown in Fig. 1, calculated from data provided by the Southeast Environmental Research Center, Florida International University (SERC-FIU), which is supported by EPA Agreement number X994621-94-0 and NOAA Agreement number NA09NOS4260253. In panels Q–T, temperature metrics were calculated from the in situ loggers and represent actual field sites used in this experiment (squares, Lower Keys; and triangles, Middle Keys). Abbreviations are: TON, total organic nitrogen; DIN, dissolved inorganic nitrogen; TOC, total organic carbon; SRP, soluble reactive phosphorous; NTU, nephelometric turbidity units; and 90%DR quantile, 90% quantile of the daily range in temperature. Significance of Mann-Whitney comparisons: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

TABLE 1. Estimate of selection against *Porites astreoides* coral transplants into the specified population at each sampling time using the percentage of mass gain as a fitness proxy in the Florida Keys, USA.

Sampling time and region	Site	Relative fitness‡	Interaction P*
Six months (Oct–Apr)			
Lower Keys	inshore	−0.10	NS
Lower Keys	offshore	0.19	NS
Middle Keys	inshore	0.20	NS
Middle Keys	offshore	−0.76	NS
One year (Oct–Oct)			
Lower Keys	inshore	0.03	<0.05
Lower Keys	offshore	0.13	<0.05
Middle Keys	inshore	0.08	NS
Middle Keys	offshore	0.04	NS

‡ Positive values indicate selection against transplants (i.e., local adaptation/acclimatization/specialization), and negative values indicate that transplants have greater fitness than the native population (i.e., maladaptation of native population).

* Significance value for origin × destination interaction term of reciprocal transplants; NS is not significant.

away" criterion for local specialization (Figs. 2 and 3). This pattern held for all cases but one (offshore to inshore transplants in the Middle Keys). The support for the "local vs. foreign" criterion was weaker, but still, for the fully reciprocal transplant pairs (i.e., cross-channel), all native populations tended to exhibit greater mass gain in comparison to foreign immigrants following one year of transplantation (Table 1, Fig. 6). Overall, these results support the hypothesis of local specialization of *P. astreoides* corals in the Florida Keys. Additionally, specialization was even more fine-scale than we initially predicted: Along-shore transplants exhibited greater reductions in fitness than cross-channel transplants (Fig. 2).

Highly structured local specialization indicates substantial environmental heterogeneity

The evidence of local specialization over distances of <10 km indicates that from the coral's perspective, the reef environment is much more heterogeneous than the SERC-monitored water quality parameters suggest (Figs. 2, 4, and 6). Previous studies involving one-way transplantation experiments between reef environments in the Florida Keys suggest similar patterns of fine-scale specialization may exist in other scleractinian coral species. In an offshore to inshore transplant of *Acropora cervicornis*, all transplants exhibited severe mortality, attributed to temperature extremes at inshore reefs (Shinn 1966). In a later experiment, offshore to inshore transplants of *Montastraea annularis* showed significantly reduced growth correlating with the distance moved inshore (Hudson 1981).

The most surprising result of this study was the response of the along-shore transplants. Every population exhibited either a significant decrease or a trend towards decrease in mass gain at every sampling time point when transplanted to these putatively environmentally similar sites (Fig. 2). Interestingly, along-shore "controls" used by Hudson (1981) at Crocker reef showed significantly reduced growth in comparison to corals left at the native Carysfort reef. In addition, growth of these along-shore transplants was also less than growth of native *M. annularis* from Carysfort (Hudson 1981), similar to patterns observed in the present study. While the effect of cross-channel transplantation varies depending on the transplantation period and is only evident after corals have experienced summer conditions at foreign reef sites (Fig. 2D, F), the consistency of growth declines upon along-shore transplantation suggests that the selective agents structuring reef habitats along-shore are likely chronic.

Daily temperature range as a potential selective agent along-shore

In attempt to provide an explanation for the unexpected growth declines in along-shore transplants, we explored a long-term water quality data set to test whether variation in coral fitness along-shore could be explained by greater variation in water quality along-shore. However, the grand majority of water quality metrics showed greater differences between cross-channel sites than between neighboring along-shore sites (Fig. 4A–S). The only metric to show consistently greater differences between along-shore sites in comparison to cross-channel sites was the 90% quantile of the daily temperature range (90%DR), reflecting the magnitude of high-frequency temperature fluctuations (Figs. 4T and 5A, B). Indeed, for offshore origin corals, this temperature metric explained a substantial portion (27–39%) of the variation in mass gain across transplant sites, suggesting that rapid temperature swings might be more detrimental for offshore-origin coral growth than the absolute high or low temperatures reached. In our experiment, inshore and offshore-novel sites demonstrated higher 90%DR in comparison to the main offshore sites (Fig. 5A, B), providing an explanation for decreased growth of offshore-origin corals transplanted there. Notably, inshore-origin corals were significantly less affected by daily temperature changes than offshore-origin corals: There was no effect of 90%DR on their growth after six months, and only 9% of growth variation was explained by 90%DR after one year. This could be the result of adaptation or acclimatization of inshore-origin corals to high variability of temperature in their home environment (Fig. 5A, B). The range of daily temperature fluctuations might therefore be a previously unrecognized agent of spatially varying selection modulating coral fitness across locations. Fluctuation-induced thermal adaptation has been documented for other coral species, although always in the context of maximal temperatures reached rather than the daily temperature ranges: Bleaching responses are reduced in populations that experienced more recent (Maynard et al. 2008) and more frequent temperature stress (Thompson and van Woesik

2009). Acclimatization of *Acropora hyacinthus* to either moderately or highly variable thermal conditions (Palumbi et al. 2014) might involve adaptation to the daily temperature range in addition to acquiring tolerance to the extreme high temperatures. However, more research will be necessary to substantiate the effect of high-frequency temperature variation on coral fitness.

Possible roles of other environmental factors

The lack of 90%DR effect on inshore-origin corals indicates that some alternative, yet unclear selective agents are responsible for along-shore growth differences of inshore-origin corals. Though cross-channel differences were always the most pronounced, for neighboring inshore reefs, four water quality metrics showed greater variation among along-shore sites in comparison to along-shore sites at offshore reefs: dissolved oxygen, salinity, turbidity, and the vertical attenuation coefficient for downward light irradiance (K_d; Fig. 5M–P), which may reflect varying exposure of inshore reefs to water inputs from "back-country" reefs. Predominant current patterns restrict water flow between inshore and offshore reefs (Smith and Pitts 2001). However, water masses from Florida Bay are capable of flowing across tidal channels (Hu et al. 2003). This source of heterogeneity may affect coral fitness patterns at neighboring inshore reef sites, though no significant differences in growth have been reported for corals that are found nearer to these channels (Lirman and Fong 2007). Additional work is needed to specifically test the effects of these candidate selective agents on coral fitness.

Though less detrimental than along-shore transplants, cross-channel transplantation also negatively impacted coral fitness (Figs. 2 and 3). Evidence from controlled laboratory experiments on nutrient loading and temperature extremes dictate that the inshore reef should be more stressful for corals (Jokiel 2004, Fabricius 2005). Yet inshore corals were consistently more negatively affected by transplantation to the offshore reef tract than offshore corals were by transplantation inshore: In three of the four comparison time points by reef region, inshore corals showed declines in growth when transplanted to offshore reefs, whereas offshore corals only exhibited a reduction in growth when moved inshore in the Lower Keys following one year of transplantation (Fig. 2C–F). One plausible explanation for this pattern involves physiological trade-offs in inshore corals that reduce their mean growth rate overall. Work on local adaptation to heavy metal pollution in other invertebrates shows a similar pattern: Tolerant populations are more fit in contaminated environments because of the greatly reduced growth of non-adapted individuals, but tolerant individuals cannot increase mean growth in unpolluted waters and are subsequently outcompeted (Piola and Johnston 2006, van Ooik and Rantala 2010). In the Florida Keys, physiological adaptations to elevated summer temperatures may underpin differential growth patterns, as trade-offs are only evident after one full year, which included summer months (Fig. 6), and temperature stress has previously been demonstrated to be a selective agent for inshore and offshore populations (Kenkel et al. 2013). In the Lower Keys, mean percentage of mass gain of inshore origin corals did not differ greatly between inshore and offshore locations across seasons (Fig. 2C, D). The offshore population, on the other hand, exhibited higher mean percentage of mass gain in the home environment and only exhibited reduced growth at the one-year sampling time point, which included summer months (Fig. 2D).

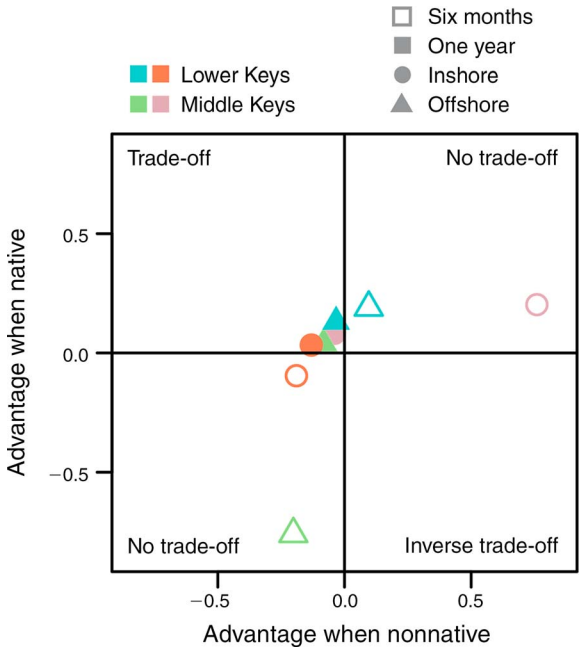

FIG. 6. Specialization to the native reef incurs trade-offs in corals transplanted to foreign environments. Each point represents a comparison between mean fitness, estimated as the relative difference in the mean percentage of mass gain, of the native population and foreign transplants at a given reef site through time ($N = 8$). Quadrants indicate separate qualitative outcomes of transplant experiments as in Bennett and Lenski (2007) and Hereford (2009). The trade-off quadrant indicates comparisons where both populations exhibited higher fitness at their native reef. The upper-right quadrant indicates populations with higher fitness at both native and foreign reefs; the lower-left shows populations exhibiting lower fitness at both native and foreign sites. The lower right quadrant indicates populations with lower fitness in the native reef environment relative to the foreign reef.

Finally, some of the unexpected growth patterns in our experiment may be attributable to environmental stochasticity. Local maladaptation is surprisingly common in natural populations and can be temporally variable (i.e., present in one year but not in another; Rice and Mack 1991, Fraser et al. 2011). In addition to seasonal temperature variation, corals in this experiment were also exposed to the stochastic effects of hurricane damage (Hurricane Isaac, August 2012), a

common disturbance on Keys reefs (Gardner et al. 2005). Middle Keys sites were more affected than Lower Keys sites, and in both regions offshore transplant sites experienced the most damage as a result of this disturbance, which may have played a role in the uniformly reduced growth observed at offshore sites in the Middle Keys.

Local specialization, trade-offs, and implications for reef conservation

Conover et al. (2006) recognized that human-induced selection that structures genotypes based on fitness can be a greater threat to genetic diversity than the direct loss of populations. This problem could be impacting reefs in the Florida Keys. Elevated nutrients and temperature extremes are not directly killing inshore populations, as corals are capable of adapting and/or acclimatizing to conditions at their native reef site (Figs. 2 and 3). However, corals must pay a cost as the underlying genetic or physiological changes necessary to maximize growth in a coral's native reef are not favored elsewhere in this ecosystem (Table 1, Fig. 6). The home site advantage observed for all focal populations of *P. astreoides* in this study indicates that specialization to the native reef comes at a cost of diminished fitness in foreign environments, implying divergent selection among habitats (Hereford 2009). The absolute magnitude of this trade-off in *P. astreoides* (yearly growth rate reduced by 7%; Table 1) is within the range of naturally observed selection pressures (Kingsolver et al. 2001). Importantly, given the longevity of reef-building corals, even such a small yearly growth disadvantage can substantially impact long-term population dynamics (Babcock 1991). In addition, other one-way transplant experiments in the Florida Keys demonstrated that *M. annularis* exhibited reductions in calcification when transplanted to novel reefs, whether along-shore or cross-channel (Hudson 1981) and *A. cervicornis* exhibited increased mortality when transplanted from offshore to inshore reefs (Shinn 1966).

Coral recruitment throughout the Caribbean is very low (Gardner et al. 2003), though adult populations release billions of viable gametes in annual mass spawning events (Levitan et al. 2004, Vize et al. 2005). Two explanations for this pattern are physical dispersal limitation and post-recruitment mortality of nonnative juveniles, or immigrant inviability (Miller et al. 2000). The increasing frequency of stochastic mortality events, for example, hurricanes (Gardner et al. 2005) or mass bleaching events (McWilliams et al. 2005), results in a loss of local populations. Concomitantly, adaptation of corals to increasingly differentiated habitats resulting from anthropogenic impacts (Pandolfi et al. 2005) may render recruits from neighboring populations unfit for recolonization of the devastated reef sites. Interestingly, recent recruitment surveys have reported that juvenile mortality, rather than a lack of recruitment, may be driving the decline of coral populations in the Florida Keys, providing support for this hypothesis (Miller et al. 2000, van Woesik et al. 2014). Taken together, this phenotype-environment mismatch (Marshall et al. 2010) may explain observed patterns of decline in the Florida Keys, though additional studies using transplants of coral juveniles of multiple species are needed to test this theory.

Trade-offs will also impact the success of reef restoration (assisted migration) efforts, which are currently ongoing in the Florida Keys (Jaap et al. 2006). The goal of assisted migration is to increase the frequency of climate adapted alleles to facilitate adaptation in future generations (reviewed in Aitken and Whitlock 2013). Temperature is assumed to be one of the largest climate change stressors impacting contemporary reefs (Hughes et al. 2003). While the genetic basis for temperature tolerance in corals is unknown, populations living in elevated temperature environments, such as inshore corals, are the most likely carriers of temperature tolerance alleles (Barshis et al. 2013). However, assisted migration can reduce fitness if local adaptation of populations also occurs in response to other environmental variables (Aitken and Whitlock 2013, Howells et al. 2013). Physiological patterns across reef sites observed in this experiment suggest that additional environmental variables are structuring coral populations in the Florida Keys. Reef managers interested in implementing assisted migration should carefully evaluate selection of source populations and transplantation sites in order to ensure that target environmental gradients are properly aligned to maximize the success of transplants and subsequent effects on gene flow. Finally, work on additional coral species is needed for the Florida Keys ecosystem, as an understanding of the extent of local specialization to climate and other environmental factors is critical for assessing the relative risks of assisted gene flow and the potential for maladaptation (Aitken and Whitlock 2013).

Conclusions

P. astreoides corals in the Florida Keys have specialized to habitats on fine spatial scales, and this specialization incurs a trade-off in the ability of these corals to grow when transplanted away from their native reef site. Of all the abiotic factors tested, coral growth patterns were best explained by the range of daily temperature fluctuations. However, knowledge of abiotic environmental gradients alone is insufficient for predicting coral fitness impacts, as inshore and offshore corals differ in their sensitivity to daily temperature variation (Figs. 2, 3, and 5). If other coral species show a similar pattern of highly structured local specialization, it will affect the success of assisted migration efforts and could prevent effective recolonization of damaged reefs, which may help explain observed patterns of coral decline in the Florida Keys. A deeper understanding of the extent of local specialization to climate and other

environmental factors will be necessary for refining management plans aimed at conserving this critically endangered ecosystem.

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Supplemental Material

Ecological Archives

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