

UC Santa Barbara

UC Santa Barbara Electronic Theses and Dissertations

Title

Incorporating Ecological Processes into Coral Reef Restoration

Permalink

<https://escholarship.org/uc/item/8v53b4w2>

Author

Ladd, Mark

Publication Date

2019

Peer reviewed|Thesis/dissertation

UNIVERSITY OF CALIFORNIA
Santa Barbara

Incorporating Ecological Processes into Coral Reef Restoration

A dissertation submitted in partial satisfaction of the
requirements for the degree Doctor of Philosophy
in Ecology, Evolution and Marine Biology

by

Mark Christopher Ladd

Committee in charge:

Professor Deron E. Burkepile, Chair

Professor Sally J. Holbrook

Professor Douglas J. McCauley

September 2019

The dissertation of Mark Christopher Ladd is approved.

Sally J. Holbrook

Douglas J. McCauley

Deron E. Burkepile, Committee Chair

July 2019

ACKNOWLEDGEMENTS

Completing this Ph.D. has been a seven-year marathon with ups, downs, excitement, frustration, success, failure, and everything in between. I could not have made it through without the support, encouragement, help, and guidance from amazing family, friends, and colleagues. Words do not begin to express how incredibly thankful I am to be surrounded by such wonderful people. To my wife, Sabrina, who has been by my side since the day we started this adventure more than seven years ago on the other side of the country, thank you. From the long days in the office to the longer days, weeks, and months away in the field, you've always been supportive, reminded me of why I got into this business in the first place, and have kept me going. I can say with certainty that I would not have made it this far without your continual patience, kindness, strength, selflessness, and love. Thank you for being the best friend I could ever imagine, I love you.

Mom and dad - thank you for always pushing me to pursue my passions and supporting me in whatever I do. Hard to believe that was a decade ago we sat on the beach in Miami and made the decision to make the switch from terrestrial to marine research. An enormous thank you to my family; Hannah, Adriano, Sam, Melissa, Maggie, and Oscar that have been there for me throughout this entire journey.

Dr. Andrew Shantz a.k.a. Poppa Shantz a.k.a. *P. shantzius* took me under his wing from the very beginning, spent countless hours teaching me how to design and setup experiments, sporcle, drive a boat, conduct field work, all while enjoying life as a PhD student. I couldn't have asked for a better mentor, field partner, friend, or brother. I'll always have fond memories of 3am starts for hell days, El Pit, Chevy Sparks, Panamanian RG-III, early morning and late-night drives to and from the keys, soda stops, and the gourmet snack isle at the top of Key Largo. "PAM". I will also always remember that you lost my new chum bag at a shark-free Conch Reef in the summer of 2014, and that we always had to drive the extra distance to get coffee at Dunkin' Donuts, even though their coffee is repulsive. I have not given up the dream of acquiring the mars rover for fieldwork, Alain's NASA research vessel, or the mobile buoy home.

Tom Adam was and continues to be an excellent mentor, colleague, and friend. I'm fortunate to have had the opportunity to work and surf alongside you and hope to continue to do so for many years to come. I will happily build cages for your any day, preferably underwater. Alain Duran's hair grew so fast that he carried a razor on board to shave his mustache between dives, he mastered the use of a magnifying glass underwater, and had the uncanny ability to leave a hammer or quadrat underwater on a daily basis. He is also one of the most positive and kindest people on Earth. Brett the "fire belcher" Pierce remains to be the only person I've seen attacked by fire coral on camera. I'm not sure how you would get so hot underwater, breath air so quickly, or vomit so violently on the boat, but you never complained and were always happy to help out in the field. James Stroud was my first friend as a PhD student, taught me about lizards, that American's love M&Ms and root beer, was always being game for trying something new and having fun. He and Kidrock never let you down when you needed them most on a Sunday in Miami. He also once lost all of his wicker patio furniture in a fiery inferno. I thank Mandy Lantz and Andark Shadd for their forthcoming scientific publications. Teenus, it's a research company, you know? Nate the Monolithic Fishmonger Lemoine always took the time to answer my questions in R, no

matter how simple or ridiculous he knew they were. Thank you for saving me the countless hours, and for all those pictures of Sasha.

Rob Nowicki was a wonderful office mate and undoubtedly had the loudest keyboard ever created by mankind. Mike Bush was an equally wonderful colleague to share an office wall with, I only wish that we had followed through with our hole idea so that we could communicate more directly and I didn't have to put you on hold through the office phone system so often. While you may have me beat in beard growing, I have been honing my skills in many other events for our eventual showdown, including; lumber selection, the carbuoy carry, timber felling, bears!, underwater hammering, the nail-grab challenge, and of course preparing for the Styrofoam levitation challenge. Marshall Sharpe has been following me around the world since 2008 and I hope he continues to do so far into the future. Ligia Collado-Vides has been a teacher, advisor, mentor, friend, and mother to me since starting my Master's in 2009. Thank you for your constant support and guidance for all things relating to life. Lady came into our lives at the perfectly right time and left us far too soon. She was there for the highest highs and the lowest lows, got us through a move across the country, being in the field for months at a time, and a stint of unemployment. Thank you for your constant source of companionship, love, and snuggles. We love you. Kaia came along just when we needed her most and has been instrumental in getting me through the final year of my Ph.D.

Hunter Lenihan always offered cold refreshments on hot walks up to the hill to the after a long day of field work, provided the JamBox, and has an impressive appreciation for reggae. Thank you for bringing me on board, providing sound life advice, a place to work, and always a good laugh. Many a night was spent with Cody Clements, Master of the 15-minute power nap and Lord of the bottle caps, labeling, epoxying, and weighing countless corals until the wee hours of the morning. You, my friend, have truly revolutionized coral reef field ecology with nothing more than a soda bottle. We will never forget ABBET. See you in the nanosphere. Katrina Munsterman showed us the ropes in Moorea back in November of 2015, made the transition to working at UCSB as painless as possible, and always made sure we had everything for a smooth and successful field season. Palmyra 2017 was an incredible experience and I'm honored to have shared it with you. Solo chub! Dana Cook, Jordan Gallagher, and Hailee Clover made the Dream Team a reality and are some of the hardest working individuals I've ever had the privilege of working alongside. Josh Manning, Q-tip, Griffin Srednick, Sam Ginther, mini-Hulk, and many other post-docs, students, and techs were exceptional station mates. Thank you to the countless undergraduates that helped with fieldwork, lab work, and made this Ph.D. possible. An enormous thank you for the support of the MCR LTER for the privilege and opportunity to work in such an amazing place with a group of wonderful people. Special thanks to Keith Seydel for being patient, keeping everything running, and having excellent hair. Erma stole my sunset tank top and wore it better than me, and Jacques and Tony taught me that you can fix things by hitting them with a hammer. Thank you to the incredible staff at Gump that made every trip to Moorea an amazing experience.

Jenn Caselle and The Aqua Twins welcomed me onto Team Palmyra, taught me to take the time to look up at the fish sometimes, and provide excellent company both on the mainland and on an island for which they constitute ~25% of the population. I hope there is an abundance of fish wrangling, cage building, and pu pus in the future. Frederick, please do not ruin our experiment.

A special thanks to the badger with a greased upper lip that frequented the late-night drive through in Miami and taught us about the proper use of ramming speed, the quality establishment that is Billy's Too, An at The Point Lounge, and Mike XXX the Magician for levitating tables and making adults believe in magic again. To all the Lobophorians that made the ultimate sacrifice in the name of science, we thank you. The Hay boat, Pickles Reef, and the many underwater viper pits throughout the Florida Keys that became a second home will forever be etched in my memory.

Thank you to my committee members Sally Holbook and Doug McCauley for your guidance and insights, and a thank you to my committee members from FIU; Ligia Collado-Vides, Margaret Miller, Elizabeth Anderson, and Mauricio Rodriguez-Lanetty for helping me develop as a scientist and student during the first three years of my PhD. Finally, a massive thank you to my advisor, Deron, for keeping me around for seven years, bringing me to California, sending me around the globe in the name of science, and providing the space and opportunities for me to develop as an individual and a scientist. I am extremely grateful for your patience, guidance, and support throughout my tenure as a graduate student.

VITA OF MARK CHRISTOPHER LADD
September 2019

EDUCATION

- Bachelor of Science in Environmental Sciences, University of Massachusetts, Amherst, May 2009 (summa cum laude)
Master of Science in Environmental Studies, Florida International University, May 2011 (summa cum laude)
Doctor of Philosophy in Ecology, Evolution and Marine Biology, University of California, Santa Barbara, September 2019 (summa cum laude)

PROFESSIONAL EMPLOYMENT

- 2014-2019: Research Assistant, Marine Community Ecology Lab, University of California Santa Barbara
2017-2019: Teaching Assistant, Department of Ecology, Evolution, and Marine Biology, Coral Reef Biology, University of California, Santa Barbara
2016 & 2019: Teaching Assistant, Department of Ecology, Evolution, and Marine Biology, Introduction to Biology II, University of California, Santa Barbara
2018: Instructor, Coral Reefs to Rainforests, University of Wisconsin Madison
2016: Teaching Assistant, Department of Ecology, Evolution, and Marine Biology, Introduction to Biology III, University of California, Santa Barbara
2014-2016: Invited Faculty, Marine Ecology, Organization for Tropical Studies
2015: Teaching Assistant, Department of Biological Sciences, General Biology I, Florida International University
2014: Teaching Assistant, Department of Biological Sciences, Advanced Marine Reserves, Florida International University
2013: Teaching Assistant, Department of Biological Sciences, General Biological Sciences II, Florida International University
2012-2014: Teaching Assistant, Department of Biological Sciences, Marine Biological Sciences and Oceanography, Florida International University
2011-2012: Adjunct Instructor, Department of Earth and Environment, Ecology of South Florida, Florida International University
2009-2011: Teaching Assistant, Department of Earth and Environment, Ecology of South Florida, Florida International University

PUBLICATIONS

- Ladd MC, Burkepile DE & Shantz AA (2019) Newly dominant benthic invertebrates reshape competitive networks on contemporary Caribbean reefs. *Coral Reefs*.
Burkepile DE, Adam TC, Ladd MC, Munsterman KS, Roycroft M & Ruttenberg B (2019) Species-specific patterns in corallivory and spongivory among Caribbean parrotfishes. *Coral Reefs*.

- Ladd MC, Burkepile DE & Shantz AA (2019) Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology*.
- Ladd MC & Burkepile DE (2018) A response to Doropoulos and Babcock. *Frontiers in Ecology and the Environment*. 16(10):559-560
- Kamath A, Pruitt JN, Brooks AJ, Ladd MC, Cook DT, Gallagher JP, Vickers ME, Holbrook SJ & Schmitt RJ (2018) Colony-level aggression and its context-specific expression contribute to coral recovery within farmerfish gardens. *Oikos*.
- Rodriguez-Casariiego J, Ladd MC, Shantz AA, Lopes C, Manjinder CS, Kim B, *et al.* (2018) Coral epigenetic responses to nutrient stress: histone H2A.X phosphorylation dynamics and DNA methylation in the staghorn coral *Acropora cervicornis*. *Ecology and Evolution*. 1-15
- Ladd MC, Miller MW, Hunt JH, Sharp W & Burkepile DE (2018) Harnessing ecological processes to facilitate coral reef restoration. *Frontiers in Ecology and the Environment*. 16(4):239-247
- Shantz AA, Ladd MC & Burkepile DE (2017) Algal nitrogen and phosphorus content drive inter- and intraspecific differences in herbivore grazing on a Caribbean reef. *Journal of Experimental Marine Biology and Ecology*.
- Ladd MC, Shantz AA, Bartels EB & Burkepile DE (2017) Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*. *Marine Ecology Progress Series*. doi: 10.3354/meps/12169
- Ladd MC, Shantz AA, Nedimeyer K & Burkepile DE (2016) Density dependence determines success of *Acropora cervicornis* restoration on a Caribbean coral reef. *Frontiers in Marine Science*. 3(261).
- Ladd MC & Shantz AA (2016) Novel enemies - previously unknown predators of the bearded fireworm. *Frontiers in Ecology and the Environment*. 14(6):342-343.
- Stroud JT, Bush MR, Ladd MC, Nowicki RJ & Sweatman J (2015) Is a community still a community? Reviewing definitions of key terms in community ecology. *Ecology and Evolution*. 5(21): 4757-4765.
- Shantz AA, Ladd MC, Schrack E & Burkepile DE (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecological Applications*. 25(8): 2142-2152.
- Stroud J, Rehm E, Olivas P, Ladd MC & Feeley K (2014) Is conservation research money being spent wisely? Changing trends in conservation research priorities. *Journal for Nature Conservation*. 22(5): 471-473.
- Ladd MC & Collado-Vides L (2013) Practical applications of monitoring results to promote coral reef resilience: A case study in the Mexican Caribbean. *Biodiversity and Conservation*. 22: 1591-1608

ABSTRACT

Incorporating Ecological Processes into Coral Reef Restoration

by

Mark Christopher Ladd

Coral reefs are the ecological, economic, and social backbone of tropical coastal communities. Yet, more than half of the world's tropical reefs are gone. With further declines predicted, there is an urgent need to develop effective solutions to resurrect degraded reefs. Part of the challenge of reef restoration is that coral reefs are extremely complex ecosystems. As such, they are often studied via a reductionist approach, whereas rebuilding an ecosystem requires a comprehensive plan to reconstruct the ecological processes necessary for a functioning reef ecosystem. Unfortunately, while we have a mechanistic understanding of many factors driving coral reef decline, there is a dearth of information available to guide us on how to restore degraded coral reefs and recover their ecosystem functions.

To this end, my dissertation examines how harnessing key ecological processes on coral reefs can facilitate the pace and success of coral reef restoration. In Chapter 1, I investigated the role of restored coral density on habitat production, and explored mechanisms contributing to density dependence in coral restoration. I found evidence of a unimodal relationship among restored *Acropora cervicornis* colonies suggesting positive density dependence at intermediate densities. Importantly, these findings highlight the fundamental role that basic restoration design elements, like outplant density, play in the success or failure of coral restoration. In Chapter 2, I assessed the importance of genotypic identity and diversity in restoration outcomes. Using a field experiment, I identified a tradeoff between

thermal-tolerance and growth rates among *A. cervicornis* genotypes, suggesting genotypic identity is a critical factor to incorporate into restoration planning.

While restoring individuals to rebuild coral populations is an important first step in coral restoration, outplanted corals do not exist in isolation when transplanted to a degraded reef. Non-scleractinian invertebrates like sponges, gorgonians, and zoanths are increasing on reefs, yet there is a paucity of data on interactions between these increasingly common organisms and corals. In Chapter 3, using observational surveys I found that competitive interactions were pervasive on Florida reefs, with 60% of sessile benthic invertebrates interacting with at least one other invertebrate. Further, results from a common garden competition experiment demonstrated that non-scleractinians like sponges and zoanths consistently outcompeted the common species *Porites porites* and *Siderastrea siderea*, suggesting competition may limit the success of these coral species and is likely to remain an important process structuring contemporary coral reef communities.

Chapter 4 addresses our knowledge gap on the effects of coral restoration on reef communities and important ecosystem functions. To do so, I conducted surveys of sites in the Florida Keys that had undergone coral restoration paired with unmanipulated control sites. I found that coral restoration enhanced coral populations, increasing coral cover 4-fold, but manifested in limited differences in coral and fish communities. Interestingly, damselfishes, whose territorial behavior may deter important processes like herbivory, were the only group of fishes that positively responded to coral restoration. These findings suggest that additional considerations beyond outplanting corals will likely be necessary to effectively restore coral reefs in a time of increasingly frequent and intense disturbances.

Lastly, in Chapter 5 I synthesized literature on coral restoration and reef ecology to identify key drivers of recovery and propose a path forward to improve coral restoration. Specifically, restoration practitioners can manipulate factors such as the density, diversity and identity of transplanted corals and leverage existing ecological processes on coral reefs to restore positive feedback processes, or disrupt negative feedback processes, and facilitate restoration success. Importantly, the results of this dissertation can be directly applied to inform how coral reef restoration is conducted and improve our ability to effectively restore degraded coral reefs.

TABLE OF CONTENTS

I. Density dependence drives habitat production and survivorship of <i>Acropora cervicornis</i> used for restoration on a Caribbean coral reef.....	1
A. Introduction.....	2
B. Methods.....	4
C. Results.....	9
D. Discussion.....	17
E. Acknowledgements.....	25
F. References.....	26
II. Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored <i>Acropora cervicornis</i>	35
A. Introduction.....	36
B. Methods.....	39
C. Results.....	44
D. Discussion.....	49
E. Acknowledgements.....	54
F. References.....	54
III. Newly dominant benthic invertebrates reshape competitive networks on contemporary Caribbean reefs.....	61
A. Introduction.....	62
B. Methods.....	64
C. Results.....	71
D. Discussion.....	78

E. Acknowledgements	85
F. References.....	85
IV. Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes	93
A. Introduction.....	94
B. Methods.....	96
C. Results	102
D. Discussion	108
E. Acknowledgements	115
F. References.....	115
V. Harnessing ecological processes to facilitate coral restoration.....	122
A. Introduction.....	123
B. Capitalizing on important ecological processes on coral reefs	128
C. Future directions and concluding remarks	139
D. Acknowledgements.....	141
E. References	142
Appendices.....	149

**I. Density dependence drives habitat production and survivorship of
Acropora cervicornis used for restoration on a Caribbean coral reef**

With Andrew A. Shantz, Ken Nedimyer, and Deron E Burkepile

Ladd, M.C., Shantz, A.S., Nedimyer, K., and Burkepile, D.E. 2016. Density dependence determines success of *Acropora cervicornis* restoration on a Caribbean coral reef. *Frontiers in Marine Science*. 3(261)

A. Introduction

Coral reefs only cover <0.1% of Earth's surface, yet house more than 30% of total marine biodiversity (Reaka-Kudla, 2005). Reefs are a key source of fisheries production (Moberg and Folke, 1999) and also provide shoreline protection for >100 million people living next to coastlines (Ferrario et al., 2014). However, the invaluable ecosystem services coral reefs provide are increasingly jeopardized as corals decline globally (Bruno and Selig, 2007; Jackson et al., 2014). In the Pacific Ocean, reefs have lost nearly half of their corals over the past four decades (Bruno and Selig, 2007). This alarming trend is even more pronounced in the Western Atlantic Ocean (henceforth, the Caribbean), where coral reefs have lost 50% of their coral cover since the mid 1970's (Gardner et al., 2003; Jackson et al., 2014). On many reefs, coral declines are accompanied by a loss of benthic diversity and increases in algae, weedy coral species, soft corals, and sponges (Burman et al., 2012; Ruzicka et al., 2013; Cardini et al., 2015). Such declines in coral cover and diversity often lead to the loss of structural complexity (Alvarez-Filip et al., 2009), diminished fish populations (Newman et al., 2015), and decreased coral recruitment (Dixson et al., 2014), jeopardizing the ecosystem function and economic value of reefs (Costanza et al., 2014).

To address these declines, coral restoration has gained increasing attention as a viable strategy to help degraded reefs recover, with large-scale restoration efforts now underway across the globe (Young et al., 2012). Current restoration efforts are primarily focused on restoring ecosystem engineers by outplanting nursery-raised corals to degraded reefs (Lirman et al., 2014; Cabaitan et al., 2015; Griffin et al., 2015). These projects have shown that coral size (Garrison and Ward, 2008), genotype (Lirman et al., 2014), and source location (Forrester et al., 2013) all influence the success of restored corals. While coral restoration is a

rapidly progressing field, significant knowledge gaps remain regarding the drivers of restoration success.

One such gap is the optimal density and arrangement for outplanting restored corals. Restoration via transplantation of autogenic ecosystem engineers in ecosystems ranging from tropical forests (Zahawi and Augspurger, 2012), to grasslands (Morgan and Scacco, 2006), to mangroves (Elster, 2000) suggests that the density and arrangement of organisms used for restoration can significantly influence their survival, growth (Li and Wilson, 1998), and recruitment (Mulligan et al., 2002). Further, the density of restored ecosystem engineers can mediate important ecological processes that drive community dynamics, such as herbivory and nutrient cycling (Holl et al., 2000).

Similarly, on coral reefs, the density and arrangement of outplanted corals will likely affect important responses such as growth rates, habitat production, disease dynamics, and, ultimately, coral survivorship. Indeed, Griffin et al. (2015) found that short-term growth rates of restored *Acropora cervicornis* over three months in the US Virgin Islands were inversely related to outplant density. In contrast, Shaish et al. (2010) found no differences in mortality or bleaching of restored *Montipora digitata* in high density, low density, or “patchy” arrangements of nursery-raised corals in the Philippines after 15 months.

Theoretical work suggests that corals outplanted in high densities and arranged with even spacing will maximize the development of topographic complexity on degraded reefs (Sleeman et al., 2005). The creation of habitat may aggregate important fishes such as schooling grunts, which can focus nutrient delivery from excretion and create nutrient hotspots that can increase the growth rates of restored corals as well as important processes such as herbivory (Shantz et al., 2015) and the removal of coral predators (Ladd and Shantz,

2016). However, there is a paucity of long-term studies that investigate the role of outplant density on coral restoration success. Given that coral restoration is an expensive and labor-intensive process, determining the most effective densities in which to outplant restored corals is an important step towards balancing the costs and benefits of coral restoration.

Here, we address this information gap by investigating the influence of coral density on the growth, habitat production, and survivorship of restored corals. Over 13 months we monitored experimentally-established populations of *Acropora cervicornis* outplanted in a gradient of densities on a reef in the Florida Keys, USA. We tracked the growth, habitat production, tissue loss, and survivorship of restored corals as proxy for the success of coral restoration. We hypothesized that low-density treatments would demonstrate higher growth rates and per-coral habitat production compared to high-density treatments. Further, we predicted that per capita tissue loss and colony mortality would be greatest in high-density plots.

B. Methods

Study Species

Acropora cervicornis is a fast-growing, branching coral species with the ability to rapidly expand via asexual fragmentation (Glynn 1973; Tunnicliffe 1981). The structural complexity provided by *A. cervicornis* and its congener, *A. palmata*, provides essential habitat for a multitude of reef-associated organisms (Reviewed in Bruckner 2002). Populations of these two species, historically structural dominants on many reefs throughout the Caribbean, have declined 80-90% in the past four decades, with drastic population reductions of >95% in some areas (Hughes 1994; Aronson & Precht 2001; Bruckner 2002; Jackson et al., 2014).

Acropora cervicornis populations have failed to recover throughout the majority of their historical range, resulting in their listing as “Threatened” under the US Endangered Species Act (Hogarth, 2006) and contributing to significant declines in structural complexity on many Caribbean reefs (Alvarez-Filip et al., 2009). Currently, coral restoration efforts are primarily focused on *A. cervicornis* due to life history characteristics amenable to rapid propagation and to the species’ critical role on Caribbean coral reefs as habitat.

Experimental Design

Our field site was a low-relief reef in ~5-7m of water located approximately 6.5km offshore of Plantation Key, Florida, USA (24.924°N, 80.503°W). We established four experimental blocks of six 4m² plots, with each plot separated by ≥5m. Each block of 4m² plots contained one replicate of each density treatment: 3-, 6-, 12-, or 24-colonies, as well as control plots in which no corals were outplanted. Each block also contained a 12-colony treatment (hereafter ‘12-clumped’), in which 12 coral colonies were outplanted within 1m² of the plot (Figure 1). Treatments were randomly assigned to plots within a block. Three *Acropora cervicornis* genotypes (K-1, K-2 and U24), obtained from the Coral Restoration Foundation’s nursery offshore of Tavernier Key, Florida, were used and present in equal (1:1:1) ratios to create experimental treatments.

To establish experimental treatments, we outplanted colonies of *A. cervicornis* approximately 85cm in total linear extension (TLE) to each plot in May of 2013. We maximized spacing among coral colonies within a plot such that colonies in low-density plots were spaced farther apart than those in high-density plots. We also organized colonies to maximize genotype mixing and avoid clumping of the same genotype. Genotype analyses,

completed as part of the Coral Restoration Foundation’s coral nursery establishment, were done using known microsatellite markers (e.g. Baums, 2008). We outplanted four replicates of each treatment in the randomized block design for a total of 228 corals outplanted into twenty-four 4m² plots. Each colony was secured to the substrate using a small amount of marine epoxy where branches contacted the reef substrate and labeled with an individually numbered tag.

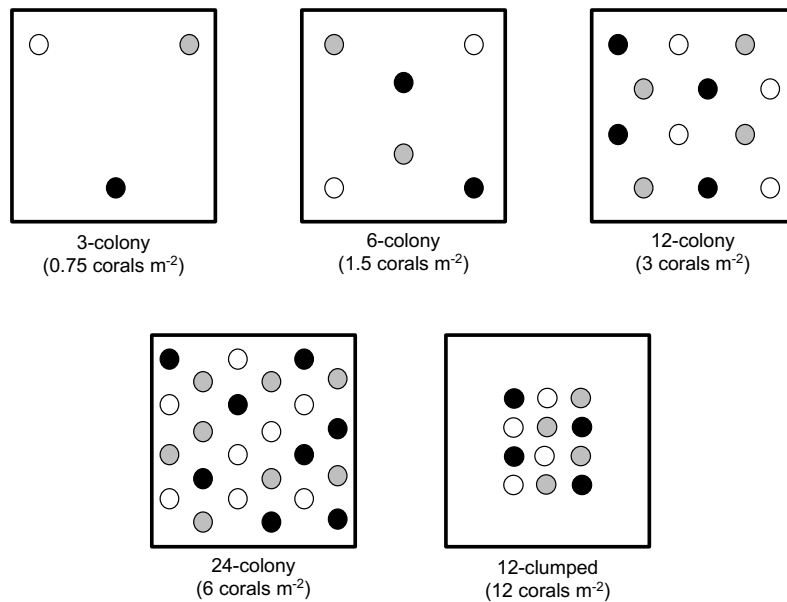


Figure 1. Schematic of experimental design (to scale). Each dot represents an individual coral outplant, different shades indicate the three unique genotypes (K-1, K-2, and U24) used to establish experimental treatments.

Coral Colony Growth, Condition and Predator Surveys

To quantify the effects of density on colony growth, we measured coral colony dimensions (length, width and height) to the nearest centimeter every 3-6 months. Surveys were conducted in May, August, and December of 2013, and June of 2014. At each sampling event, we also recorded the percent of each coral colony without live tissue and the presence of any disease-like symptoms (e.g., rapid tissue loss, white band disease) via visual

assessment. We also counted corallivorous snails (*Coralliophila abbreviata*) and fireworms (*Hermodice carunculata*) on each *A. cervicornis* colony. However, these predators and instances of disease were so rare that we did not explore these data quantitatively.

Statistical Analyses

We estimated total skeletal linear extension (TLE; the sum of the lengths of all branches on a colony) using length, width, and height conversions provided by Kiel et al. (2012). To calculate per capita live TLE for each survey period we used the equation:

$$\text{per capita live TLE} = \text{colony total TLE} - (\text{colony total TLE} \times \% \text{ of colony without live tissue})$$

Growth rates were calculated for each interval by dividing the TLE accumulated between survey periods by the number of days elapsed to generate a daily growth rate. For all growth rate and TLE calculations, data for corals were not included if: (1) they showed signs of previous breakage, a common natural occurrence in *A. cervicornis* corals, or (2) displayed 100% tissue loss, which avoided artificially depressing growth rates or TLE measures. We calculated TLE and live TLE at the plot level by summing measures of TLE or live TLE for all corals within a plot. We then used these measures to compare total habitat production (using TLE as a proxy) and live TLE among treatments.

We assessed changes through time in growth rates, per capita TLE, and per capita live TLE via a nested two-way repeated measures ANOVA that considered time and treatment or genotype as predictors and included an interaction between the main factors. For these analyses individual corals were nested within a plot and considered as a random effect to avoid violating assumptions of independence. Among treatment differences within individual survey periods were analyzed via post-hoc tests with Tukey's corrections using the *multcomp* package in R (Hothorn et al., 2008). Because of the non-normal structure of the tissue loss

data, we used a Kruskal-Wallis test with post-hoc analysis to compare median values of the percent of colony without live tissue among treatments at each survey period.

Treatment survivorship was calculated using the percentage of colonies that were alive within a plot at each survey period. Genotype survivorship was calculated as the percentage of coral colonies for each genotype that remained alive at a given survey point. A coral was considered dead when it had no living tissue on the skeleton. Among treatment differences in survivorship, plot level TLE, and plot level live TLE were analyzed via a two-way ANOVA that considered treatment and time as predictors with an interaction between the main factors. Among treatment differences within individual survey periods were analyzed via post-hoc tests with Tukey's corrections using the *multcomp* package in R (Hothorn et al., 2008). Among genotype differences in survivorship at the end of the experiment were analyzed via a Fisher's Exact Test, followed by pairwise comparisons of the three genotypes using a Bonferonni correction. Colony growth rates and per capita live TLE were square-root transformed, while per capita TLE, plot level TLE, and plot level live TLE were log-transformed to meet ANOVA assumptions.

To investigate the presence of density dependent effects among treatments, we compared treatments that differed two-fold in coral density by calculating ratios of final plot level TLE (i.e. 6-colony vs. 3-colony treatments). To generate conservative estimates, we first ranked plots within a treatment from highest to lowest plot level TLE. We then paired plots according to ranks and then divided the final plot level TLE of one treatment by the final plot level TLE of the treatment with half the number of corals (e.g. 6-colony/3-colony). If there were no density dependent effects, we expected that a doubling of coral density would result in a doubling of TLE. Thus, if density dependence did not influence habitat production, we

expected a ratio of 2:1 for plot level TLE. A ratio >2 would indicate positive density dependence (i.e. a doubling of coral density resulted in more than a doubling in TLE) while a ratio <2 would suggest negative density dependence (i.e. a doubling of colony density resulted in less than a doubling in TLE). We also compared the 12-clumped and 12-colony final plot level TLE to assess the effect of arrangement. For this comparison, if density did not influence habitat production, we expected a ratio of 1:1, since both treatments contained 12 corals. We used a two-tailed t-test to determine if ratios were significantly different from two, the expected doubling in TLE from a doubling of density (or one in the case of the 12-clumped vs. 12-colony comparison). We conducted these comparisons for both plot-level TLE and plot-level live TLE. We computed a Pearson product-moment correlation coefficient to assess the relationship between the density of corals and proportion of corals alive within a treatment at the end of the experiment. All analyses were conducted in R version 3.0.2 (R Core Team, 2013). All data reported are means \pm SE.

C. Results

Genotype Effects

Genotype had no effect on restored coral growth rates, total linear extension (TLE), or live TLE at any point during the experiment (Appendix 1). At the conclusion of the experiment, genotype had a marginal effect on the mean percent of a colony with no live tissue (Genotype effect: $F_{2,189} = 2.649$, $p = 0.073$) and survivorship of restored corals (Fisher's Exact Test, $p = 0.078$; Appendix 2). Genotype K-1 was trending towards lower survivorship and having less live tissue per colony. However, genotype appeared to have little influence on coral growth and survivorship as compared to treatment effects described below.

Density Effects

Growth rates of individual corals varied among treatments more than three-fold, from a low of 0.248 cm day⁻¹ to a high of 0.829 cm day⁻¹ (mean \pm SE; 0.49 \pm 0.016), and showed a significant time by treatment interaction ($F_{8,222} = 4.694$, $p < 0.001$; Figure 2). Complete statistical results are provided in Appendix 3. Post-hoc tests with Tukey's correction revealed that while growth rates were statistically indistinguishable from May to December 2013, corals in the 12-colony treatments grew nearly two times faster than corals in 24-colony treatments from December 2013 to June 2014 ($p = 0.035$). All of the other treatments also had $\geq 50\%$ greater mean growth rates than the 24-colony treatment during this time period, but post-hoc tests did not detect statistical differences likely due to high variability in growth rates.

Both per capita total linear extension (Treatment x Time effect: $F_{12,476} = 3.96$, $p < 0.001$; Figure 3 top) and per capita live total linear extension (Treatment x Time effect: $F_{12,476} = 13.322$, $p < 0.001$; Figure 3 bottom) differed among treatments through time. However, post-hoc tests indicated that the only among treatment differences were for live TLE at the final (June 2014) sampling period where corals from 12-colony treatments had nearly 3x more live TLE than those in the 24-colony treatments ($p = 0.03$). The other treatments were intermediate in live TLE and did not differ from either the 12- or 24-colony treatments. The patterns for TLE were similar but post-hoc tests did not show statistically significant differences. Median values for percent of colony without live tissue were significantly higher for corals within the 12-clumped and 24-colony treatments as compared to 3- and 12-colony treatments ($\chi^2 = 43.07$, $df = 4$, $p < 0.001$; Figure 4). Further, we found clear effects of density treatment on restored coral survivorship (Treatment x Time effect: $F_{16,72} = 4.108$, $p < 0.001$;

Figure 5), with survivorship significantly decreasing with increasing density. The 12-clumped treatment had the highest initial mortality rates (August 2013) and ended up losing ~50% of individual colonies by the end of the experiment, similar to that of the 24-colony treatment. On the other extreme, the 3-colony treatment had 100% survivorship for the duration of the experiment. At the conclusion of the experiment, colony survivorship was negatively correlated the density of corals (Pearson's product-moment correlation coefficient, $r = -.085$, $df = 3$).

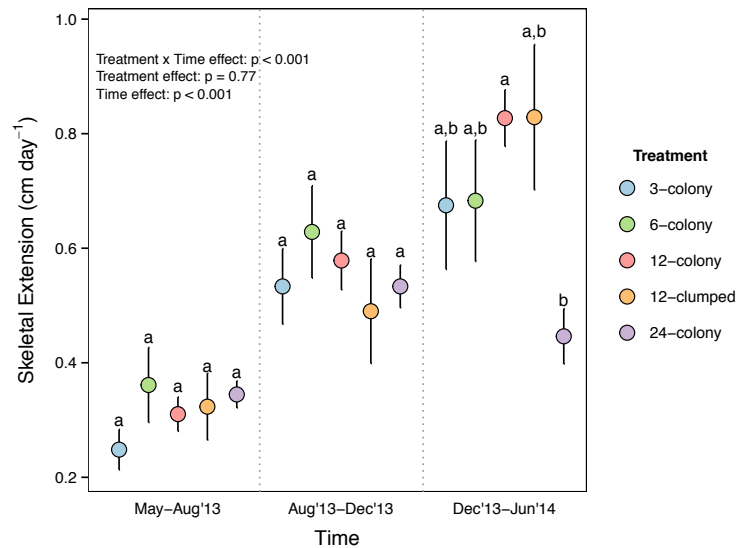


Figure 2. Daily growth rate (cm day^{-1}) of individual corals by treatment through time. Labels on x-axis indicate the time period over which growth rates were calculated. Statistics are from nested two-way repeated measures ANOVA. Letters represent significant differences ($p < 0.05$) among treatments within a time period from post-hoc tests with Tukey's correction. Data are means \pm SE.

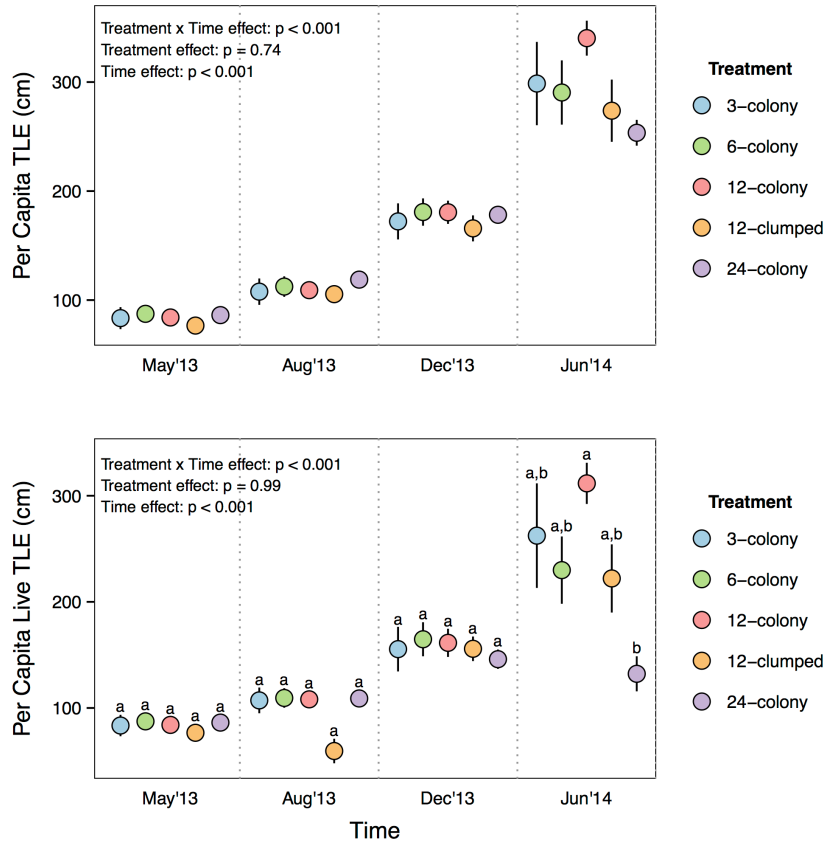


Figure 3. (top) Per capita total linear extension (TLE) and (bottom) per capita live TLE of individual corals by treatment through time. Labels on x-axis indicate the time at which each survey was conducted. Statistics are from nested two-way repeated measures ANOVA. Letters represent significant differences ($p < 0.05$) among treatments within a time period from post-hoc tests with Tukey's correction. Data are means \pm SE.

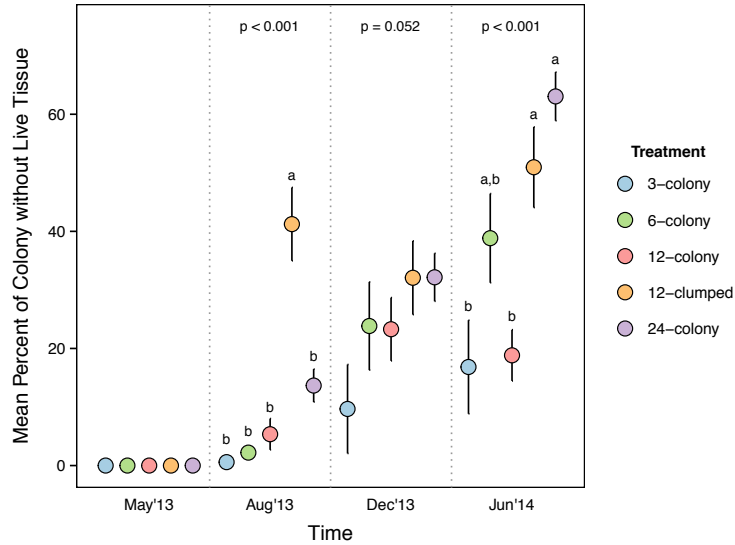


Figure 4. Percent of each coral colony without live tissue compared among treatments within each survey period. P-values for each survey period are from Kruskal-Wallis test. Letters represent significant differences ($p < 0.05$) among treatments from post-hoc analysis comparing median percent of colony without live tissue values within a survey period. Data are means \pm SE.

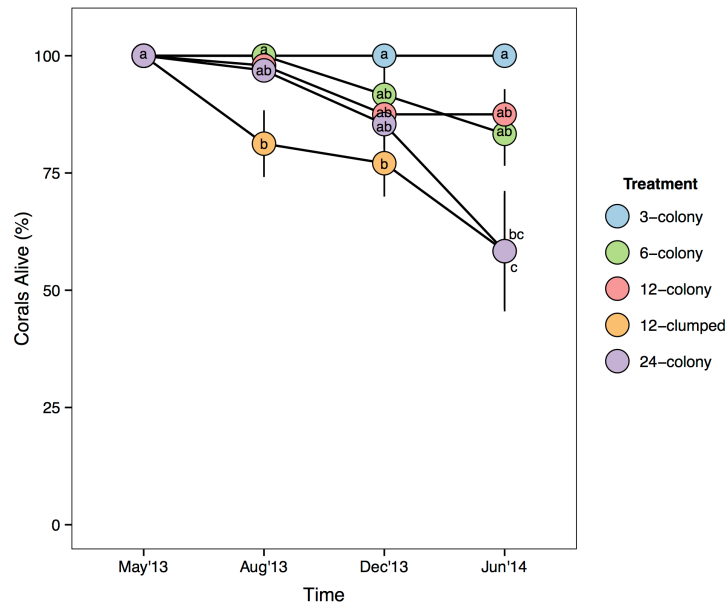


Figure 5. Mean survivorship of coral colonies by treatment over time. Statistics are from nested two-way repeated measures ANOVA. Letters represent significant differences ($p < 0.05$) among treatments within a time period from post-hoc tests with Tukey's correction. Data are means \pm SE.

The differences in per capita live TLE resulted in the 12- and 24-colony treatments ending with similar overall habitat production (plot-level TLE) by the end of the experiment, despite the 12-colony treatment starting the experiment with half the number of corals (Treatment x Time effect: $F_{12,60} = 1.193$, $p = 0.309$; Figure 6 top). The patterns in plot-level live TLE were similar to overall TLE, showing significant Treatment x Time effects ($F_{12,60} = 2.240$, $p = 0.02$; Figure 6 bottom). Similar to the overall plot-level TLE, the 12- and 24-colony treatments showed similar levels of live TLE. Surprisingly, within three months 6-colony treatments had produced as much live TLE at the plot level as 12-clumped treatments.

Analyzing these dynamics over time within treatments showed several interesting patterns. All treatments except the most dense (12-clumped) increased in plot level TLE during the course of the experiment (Figure 7 top). On average, 24-colony treatments did not accumulate live TLE at the plot level during the course of the experiment (Time effect: $F_{3,12} = 0.10$, $p = 0.956$; Figure 7 bottom) as tissue loss appeared to occur at the same rate as tissue growth. Similarly, 12-clumped treatments actually decreased in live TLE from May to August of 2013, then rebounded to initial levels by December 2013. Conversely, 12-, 6- and 3-colony treatments significantly increased in plot level live TLE throughout the course of the experiment. The largest increase relative to initial TLE was seen in 12-colony treatments, which more than tripled the amount of live TLE by the end of the experiment.

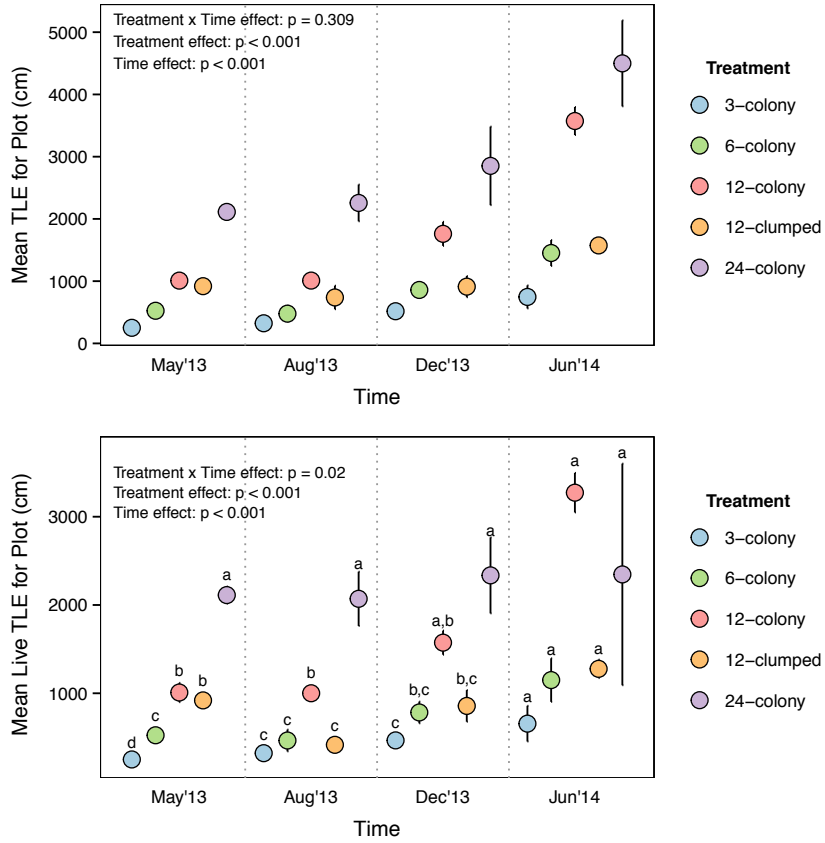


Figure 6. (top) Total linear extension and (bottom) live TLE at the plot level comparing among treatments across each survey period. Statistics are from nested two-way repeated measures ANOVA. Letters represent significant differences ($p < 0.05$) among treatments within a time period from post-hoc tests with Tukey's correction. Data are means \pm SE.

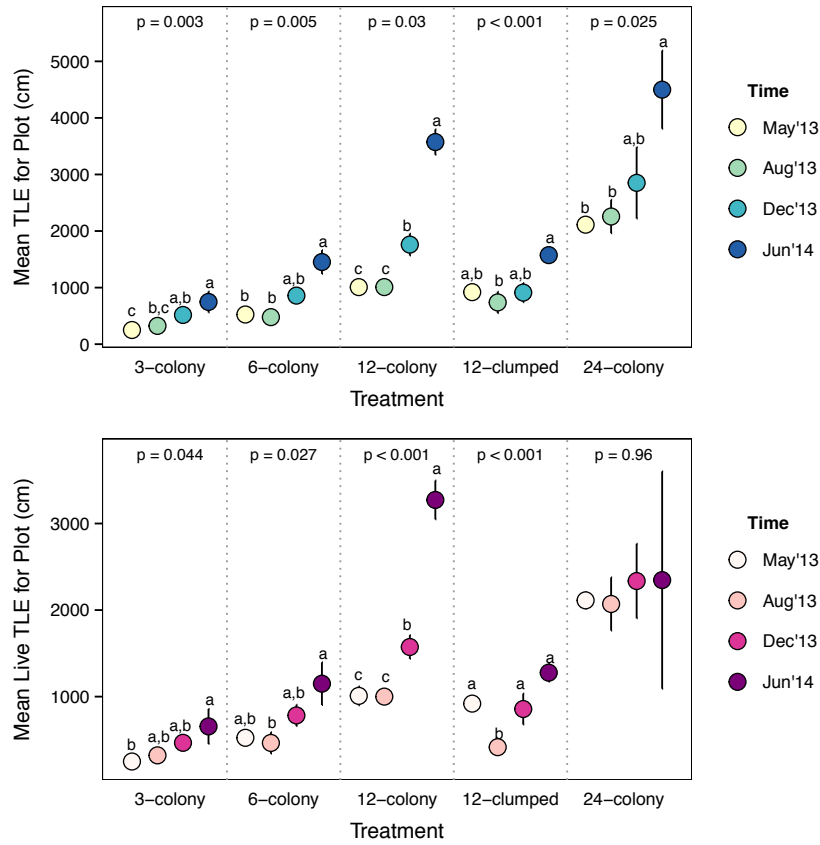


Figure 7. (A) Total linear extension and (B) live TLE at the plot level comparing among survey periods within each treatment. Statistics are from one-way ANOVA. Letters represent significant differences ($p < 0.05$) among time periods within a treatment from post-hoc tests with Tukey's correction. Data are means \pm SE.

We found evidence of density dependent effects when we compared final habitat production (both TLE and live TLE) between treatments. For both TLE and live TLE, the 12-clumped vs. 6-colony and 24- vs. 12-colony comparisons demonstrated negative density dependence, evidenced by the nearly 1:1 ratio of TLE at the end of the experiment compared to the expected 2:1 ratio (Figure 8). Similarly, both TLE and live TLE in 12-clumped (12 corals m^{-2}) treatments demonstrated strong negative density dependence compared to the less dense 12-colony (3 corals m^{-2}) with ratios significantly lower than the expectation of 1:1. There was also evidence for positive density dependence, but it was less strong. The 12-colony treatments had on average 2.5 times and 3 times more TLE and live TLE than 6-

colony treatments, respectively, although both tests for a difference from the 2:1 ratio were marginally significant ($p = 0.07$ for TLE and $p = 0.09$ for live TLE).

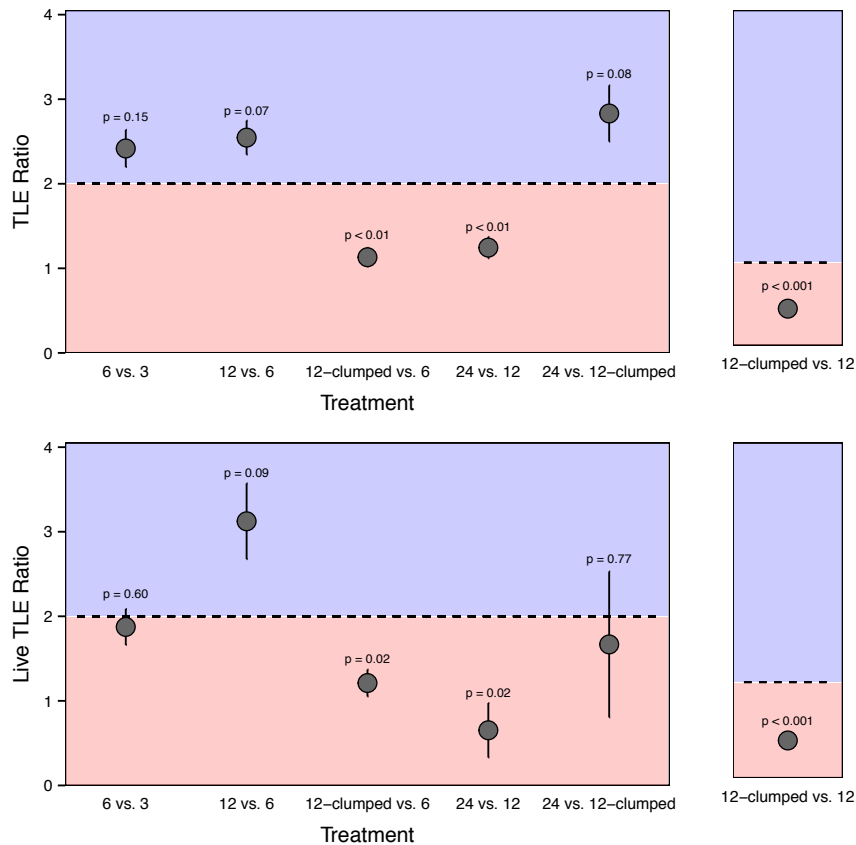


Figure 8. Ratios comparing final plot level (top) TLE and (bottom) live TLE between treatments differing in coral density. Comparisons are either between treatments that differ two-fold in coral density (e.g. 6-colony vs. 3 colony treatments; left panels) or with equal densities (12-clumped vs. 12-colony treatments; right panels). The black dotted line represents the expected 2:1 (right panels) or 1:1 ratio (left panels). Points that fall within the blue shaded area exceeded expectations of habitat production and suggest positive density dependence. Points that fall within the red shaded area produced less habitat than predicted and suggest negative density dependence.

D. Discussion

As coral reefs continue to decline globally (Bruno and Selig, 2007; Jackson et al., 2014), the need to develop effective strategies to restore degraded reefs is becoming increasingly urgent. Although coral restoration has gained increased attention as a viable strategy to restore reefs, it remains a labor- and cost-intensive strategy (Young et al., 2012; Rinkevich,

2014). Thus, there is a need to maximize ecological benefits while minimizing costs to continue scaling up coral restoration efforts. Here, we show that coral outplant density is a key factor to the success of coral restoration. We found that the survivorship of restored corals decreased with increasing density. Corals outplanted in moderate densities (12-colony treatments; 3 corals m^{-2}) grew faster and lost less live tissue than high-density (24-colony and 12-clumped treatments; 6 and 12 corals m^{-2}) treatments. Further, corals in 12-colony treatments tripled in total linear extension (TLE) during the course of the experiment and on average ended up with more live TLE at the plot level as compared to 24-colony treatments, though they started the experiment with half the number of corals. Importantly, our data suggest the presence of both positive and negative density dependent effects. Increasing density to 3 corals m^{-2} resulted in more coral growth than expected. But, continuing to add more corals (6 or 12 corals m^{-2}) resulted in negative density dependence and less coral growth than expected.

Despite substantial evidence of the impact of coral genotype on coral growth rates, survivorship, and disease prevalence (Vollmer and Kline, 2008; Lirman et al., 2014), we found no effect of genotype on any of our response variables. Instead, we show that density dependence plays a large, yet underappreciated, role in the success or failure of coral restoration efforts. Although we found stronger density effects than genotype effects, we only used three genotypes of *A. cervicornis*. Promoting genotypic diversity should still remain a restoration priority. Given the uncertain conditions reefs are likely to experience in the future (Pandolfi, 2015; Pendleton et al., 2016), including genotypes with a range of traits and environmental tolerances will likely be essential for successful coral reef restoration.

Density often influences the success of restoring ecosystem engineers in other ecosystems (Li and Wilson, 1998; Holl et al., 2000; Mulligan et al., 2002). Yet, limited research on the role of density exists for coral restoration, particularly in the Caribbean. Our findings suggest that outplanting *A. cervicornis* for restoration in moderate densities (3 corals m⁻² – our 12-colony treatment) maximizes growth rates and habitat production while minimizing tissue loss and coral mortality. To our knowledge, the only other study that manipulated the density of *A. cervicornis* colonies found a negative relationship between coral density and linear extension (Griffin et al., 2015). However, this study only tracked corals for a period of three months, had limited replication (n=1 per density), and potentially confounded density effects with genotype effects. The longer (13 month) duration of our study allowed us to elucidate the effect of the density of restored corals over timescales more relevant to coral reef community recovery. Similar to Griffin et al. (2015), we found that growth rates in our 24-colony treatment were lower than the others at the end of the experiment. However, we show that density dependence can influence the success of *A. cervicornis* outplanted for restoration, and that the strength and direction of density dependence changes with coral density. These findings run counter to work done in the Philippines, which found no effect of outplant density or arrangement on *Montipora digitata* growth or mortality over a 15-month study, suggesting different species may display variable responses to outplant density (Shaish et al., 2010).

Density dependence has been heavily studied in terrestrial and intertidal systems, often with a particular focus on foundation species (Bertness and Callaway, 1994; Bruno et al., 2003). Work in marine systems, and specifically coral reef ecosystems, has largely focused on the effects of density dependence on the growth and survivorship of coral-associated

organisms, such as coral reef fishes, rather than corals themselves (Hixon and Carr, 1997; Hixon and Webster, 2002; but see Baird and Hughes, 2000; Shantz et al., 2011; Marhaver et al., 2013). Here, we found that the densities of our densest treatments resulted in less habitat creation and live coral tissue than would be expected, suggesting negative density dependence.

Although TLE and live TLE increased for the 3-colony, 6-colony, and 12-colony plots, the densest treatments (12-clumped and 24-colony) saw little to no increase in these metrics over our 13-month study. Several mechanisms could be important for driving this negative density dependence. While small-scale alterations in water flow may benefit corals growing in close proximity, at some density threshold, such as in our 24-colony or 12-clumped treatments, coral branches could become so dense as to have a negative effect on water flow. At such high densities, reductions in water flow may reduce mass transfer of nutrients to the coral or efflux of oxygen as a byproduct of photosynthesis, contributing to declines in photosynthesis and the energy available for coral growth (Finelli et al., 2006). Additionally, crowding in high-density treatments could increase shading and intensify competition for light, effectively reducing photosynthesis (Chadwick and Morrow, 2011). Although *A. cervicornis* relies heavily on photosynthetic endosymbionts for energy, heterotrophic feeding is an important component of growth rates, particularly under stressful conditions (Houlbrèque and Ferrier-Pagès, 2009; Towle et al., 2015). Thus, corals in high-density plots may have experienced increased competition for food particles in the water column, contributing to lower growth rates in these treatments.

Additional mechanisms likely contributed to the negative density-dependent effects at the high-density treatments. High densities of corals may facilitate disease transmission among

coral colonies. Some coral diseases can be vectored between *A. cervicornis* branches that are in direct contact (Williams and Miller, 2005). Thus, disease transmission may have been facilitated in 24-colony and 12-clumped treatments where branches of colonies were more likely to be in direct contact as compared to lower density treatments. The corallivorous snail *Coralliophila abbreviata*, and the fireworm *Hermodice carunculata* can vector or act as a reservoir for coral diseases (Sussman et al., 2003; Williams and Miller, 2005; Gignoux-Wolfsohn et al., 2012). Consequently, these coral predators, which commonly feed on *A. cervicornis* (Miller, 1981), may cause initial disease infection or spread diseases within a plot of restored corals. Tightly clustered colonies in high-density treatments may have provided a physical escape from predation for small corallivores, increasing the probability of tissue loss and infection. Further, *C. abbreviata* prefers *A. cervicornis* colonies surrounded by conspecifics rather than solitary colonies or those surrounded by heterospecifics (Johnston and Miller, 2014), suggesting that high-density treatments may be preferred by corallivores.

While we did record predator density and disease presence as part of this study, our surveys were not frequent enough to track disease progression or link tissue loss to predator abundance. Although variable among replicates, we observed an average of 30% of corals showing signs of disease (rapid tissue loss) in 12-clumped treatments during our August 2013 survey, which coincided with significant increase in live tissue loss (Figure 4). Thus, the densest treatment appeared to facilitate disease, leading to dramatic loss of live coral. Partial colony mortality, highest in the 12-clumped and 24-coral treatments at the end of the experiment, likely depressed growth rates and contributed to the negative density-dependent effects we observed in the high-density treatments.

Farming damselfish (e.g., *Stegastes planifrons*) can rapidly colonize *A. cervicornis* colonies outplanted for restoration, cause significant amounts of partial mortality, and decrease coral growth rates (Schopmeyer and Lirman, 2015). While we did not specifically quantify damselfish abundance in our experiment, we also did not observe strong colonization by farming damselfish in our study. However, damselfish may selectively recruit to high-density plots that provide more shelter from predators (Almany, 2004) and substrate to create their algal lawns (Ceccarelli et al., 2001). Thus, at other restoration sites, the colonization of high-density coral treatments by territorial damselfish could be an additional mechanism contributing to negative density-dependence of corals used for restoration.

Although our analyses showed only marginally significant effects for positive density dependence, the patterns were suggestive of positive effects of increasing density to moderate levels. This pattern was most obvious going from the 6-colony to the 12-colony densities where TLE and live TLE increased 2.5 to 3 times. These data suggest the existence of positive feedback mechanisms for coral growth and habitat creation under moderate increases in density. For corals, more live tissue affords increased opportunity for growth, and therefore increasing structural complexity, particularly for branching corals such as *A. cervicornis*. Positive density dependence could also be expected for corals through the improvement of microclimatic conditions, as observed for plants in terrestrial systems (Bruno et al., 2003). For example, increased coral density could decrease laminar flow and increase mixing, reducing the boundary layer and enhancing delivery of nutrients and dissolved oxygen to nearby corals (Atkinson and Bilger, 1992; Lesser et al., 1994). For species that rely heavily on asexual fragmentation, such as *A. cervicornis*, high densities can function to

trap and stabilize asexual fragments, contributing to a positive density dependent feedback (Tunncliffe, 1981). Over time branches can fuse together to form dense thickets that increase resistance to physical disturbance and further promote fragment retention.

Reef fishes, often limited by habitat availability as both juveniles and adults, selectively recruit to live coral, where they grow faster than fishes recruiting to non-living structure (Holbrook et al., 2000; Feary et al., 2009; Kerry and Bellwood, 2015). The topographic complexity provided by corals can aggregate fishes, concentrating fish-derived nutrients that can increase coral growth (Holbrook et al., 2008; Shantz and Burkepile, 2014). These fish-derived nutrient hotspots also increase grazing by herbivorous fishes and decrease algal abundance, both of which likely help facilitate coral growth and survivorship (Shantz et al., 2015). Further, many of the fishes that aggregate around structurally complex corals are invertivores, such as white grunts (*Haemulon plumierii*), possibly promoting top-down control on coral predators (Lirman, 1999; Ladd and Shantz, 2016).

Our findings have important implications for how we approach coral restoration. Ultimately, the goal of coral restoration is to promote ecological processes and positive feedbacks that foster self-sustaining coral reef communities. While the goal of coral restoration is not focused solely on corals, these ecosystem engineers are the foundation upon which other essential species and ecological processes depend (Mumby and Steneck, 2008; Newman et al., 2015). For example, coral and fish larvae are able to track the smell of corals to use as positive settlement cues (Dixson et al., 2014). Larger corals also have higher reproductive potential (Szmant, 1986), and therefore are more likely to contribute to sexual reproduction, a key component of coral reef recovery. Thus, restoration efforts that maximize

coral growth, coral survivorship, and habitat creation will likely promote these important positive feedbacks and more quickly foster the recovery of coral reef communities.

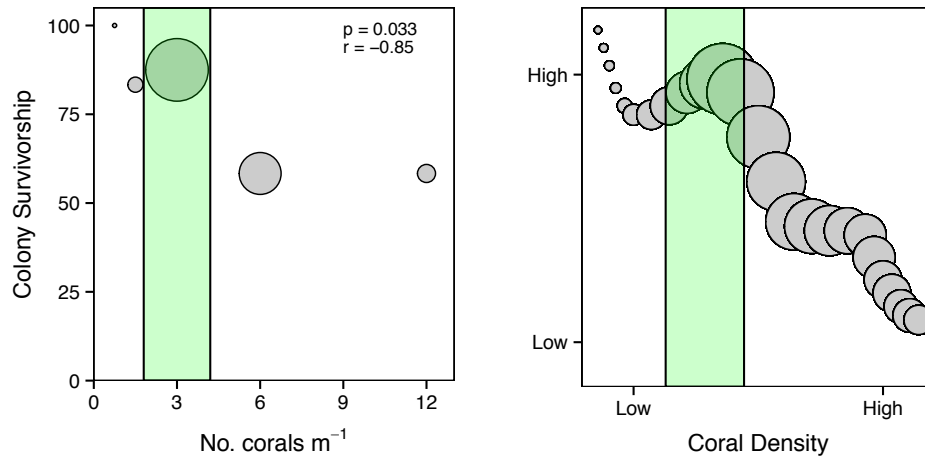


Figure 9. (left) Relationship between the density of *A. cervicornis* outplanted for restoration and colony survivorship. The size of each point is scaled to the average amount of live TLE (i.e. habitat created) for each treatment at the conclusion of the experiment. The green area represents the densities over which positive density dependence may facilitate coral survivorship and habitat production. Statistics from Pearson’s product-moment correlation (df = 3). (Right) Proposed relationship between the density of *A. cervicornis* outplanted for restoration, colony survivorship, and habitat production. Points are scaled to the amount of live habitat created, thus larger circles represent more habitat generation. The green area highlights densities where restoration practitioners can take advantage of positive density-dependence to maximize the benefits of coral restoration.

Here, we show that the direction and intensity of density dependence on the success of corals used for restoration is context-dependent. These findings highlight the need for restoration practitioners to consider the density of corals when planning restoration efforts. For *A. cervicornis*, the primary species used for coral restoration in the Caribbean, our data suggests that outplanting in densities of three corals m⁻² can take advantage of positive density dependent processes that maximize habitat production and reduce mortality (Figure 9 left). We posit that by capitalizing on positive density-dependent processes, restoration practitioners can maximize the benefits of coral restoration (Figure 9 right). Further, this would avoid overloading areas with corals that could be used to restore other areas. Importantly, we found that increasing the density of coral to 6 or 12 corals m⁻² can actually induce negative density dependent processes that increase coral mortality and slow coral

growth, working against restoration goals. These results demonstrate the need to evaluate the influence of density on the success of other coral species used for restoration, which likely display density-dependent relationships that could be exploited to facilitate coral restoration. Further work is needed to determine the effect density has on important factors such as disease transmission and predator attraction as well as ecosystem processes such as herbivory and nutrient recycling that will likely also influence coral restoration success. Long-term studies investigating how the density of corals influences the development of coral reef communities and the ecological processes that maintain healthy reefs will advance our ability to effectively restore coral reef communities.

E. Acknowledgments

Funding for this work was provided by a Florida Sea Grant Scholar award (PD-12-20) and a Friends of Gumbo Limbo Gordon Gilbert Graduate Research Grant to MCL, and was facilitated by a grant from the National Science Foundation, Biological Oceanography program (OCE-1130786) to DEB. This work was conducted with permission from the Florida Keys National Marine Sanctuary under permit no. FKNMS-2012-134. We thank the Coral Restoration Foundation for providing the *Acropora cervicornis* colonies and fieldwork assistance. We thank A. Durán, E. Shaver, B. Pierce, A. Zenone, B. Gunn, C. Lopes, and C. Fuchs and many others for assistance in the field.

F. References

- Almany, G. R. (2004). Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141, 105–113.
doi:10.1007/s00442-004-1617-0.
- Alvarez-Filip, L., Dulvy, N. K., Gill, J. A., Côté, I. M., and Watkinson, A. R. (2009). Flattening of Caribbean coral reefs: region-wide declines in architectural complexity. *Proc. R. Soc. B* 276, 3019–25. doi:10.1098/rspb.2009.0339.
- Aronson, R., and Precht, W. (2001). White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460, 25–38.
- Atkinson, M. J., and Bilger, R. W. (1992). Effects of water velocity on phosphate uptake in coral reef-flat communities. *Limnol. Ocean.* 37, 273–279. doi:10.4319/lo.1992.37.2.0273.
- Baird, A., and Hughes, T. (2000). Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *J. Exp. Mar. Bio. Ecol.* 251, 117–132.
- Baums, I. B. (2008). A restoration genetics guide for coral reef conservation. *Mol. Ecol.* 17, 2796–811. doi:10.1111/j.1365-294X.2008.03787.x.
- Bertness, M. D., and Callaway, R. (1994). Positive interactions in communities. *Trends Ecol. Evol.* 9, 191–3. doi:10.1016/0169-5347(94)90088-4.
- Bruckner, A. W. (2002). Proceedings of the Caribbean *Acropora* Workshop : Potential Application of the U.S. Endangered Species Act as a Conservation Strategy. Silver Spring, MD.
- Bruno, J. F., and Selig, E. R. (2007). Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2, e711.

doi:10.1371/journal.pone.0000711.

Bruno, J. F., Stachowicz, J. J., and Bertness, M. D. (2003). Inclusion of facilitation into ecological theory. *Trends Ecol. Evol.* 18, 119–125. doi:10.1016/S0169-5347(02)00045-9.

Burman, S., Aronson, R., and van Woesik, R. (2012). Biotic homogenization of coral assemblages along the Florida reef tract. *Mar. Ecol. Prog. Ser.* 467, 89–96. doi:10.3354/meps09950.

Cabaitan, P. C., Yap, H. T., and Gomez, E. D. (2015). Performance of single versus mixed coral species for transplantation to restore degraded reefs. *Restor. Ecol.*, 1–8. doi:10.1111/rec.12205.

Cardini, U., van Hoytema, N., Al-Rshaidat, M. M. D., Schuhmacher, H., Wild, C., and Naumann, M. S. (2015). 37 Years later: revisiting a Red Sea long-term monitoring site. *Coral Reefs* 34, 1111. doi:10.1007/s00338-015-1321-z.

Ceccarelli, D. M., Jones, G. P., and McCook, L. J. (2001). Territorial damselfishes as determinants of the structure of benthic communities on coral reefs. *Oceanogr. Mar. Biol.* 39, 355–389.

Chadwick, N. E., and Morrow, K. M. (2011). “Competition Among Sessile Organisms on Coral Reefs,” in *Coral Reefs: An Ecosystem in Transition*, eds. Z. Dubinsky and N. Stambler (Dordrecht: Springer Netherlands), 347–371. doi:10.1007/978-94-007-0114-4.

Costanza, R., de Groot, R., Sutton, P., van der Ploeg, S., Anderson, S. J., Kubiszewski, I., et al. (2014). Changes in the global value of ecosystem services. *Glob. Environ. Chang.* 26, 152–158. doi:10.1016/j.gloenvcha.2014.04.002.

Dixson, D. L., Abrego, D., and Hay, M. E. (2014). Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery. *Science*. 345,

892–897. doi:10.1126/science.1255057.

Elster, C. (2000). Reasons for reforestation success and failure with three mangrove species in Colombia. *For. Ecol. Manage.* 131, 201–214. doi:10.1016/S0378-1127(99)00214-5.

Feary, D. A., McCormick, M. I., and Jones, G. P. (2009). Growth of reef fishes in response to live coral cover. *J. Exp. Mar. Bio. Ecol.* 373, 45–49. doi:10.1016/j.jembe.2009.03.002.

Ferrario, F., Beck, M. W., Storlazzi, C. D., Micheli, F., Shepard, C. C., and Airoidi, L. (2014). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat. Commun.* 5, 3794. doi:10.1038/ncomms4794.

Finelli, C. M., Helmuth, B. S. T., Pentcheff, N. D., and Wethey, D. S. (2006). Water flow influences oxygen transport and photosynthetic efficiency in corals. *Coral Reefs* 25, 47–57. doi:10.1007/s00338-005-0055-8.

Forrester, G. E., Taylor, K., Schofield, S., and Maynard, A. (2013). Colony growth of corals transplanted for restoration depends on their site of origin and environmental factors. *Mar. Ecol.* 34, 186–192. doi:10.1111/maec.12000.

Gardner, T., Côté, I., Gill, J., Grant, A., and Watkinson, A. (2003). Long-term region-wide declines in Caribbean corals. *Science.* 301, 958–960.

Garrison, V., and Ward, G. (2008). Storm-generated coral fragments - A viable source of transplants for reef rehabilitation. *Biol. Conserv.* 141, 3089–3100. doi:10.1016/j.biocon.2008.09.020.

Gignoux-Wolfsohn, S., Marks, C. J., and Vollmer, S. V (2012). White Band Disease transmission in the threatened coral, *Acropora cervicornis*. *Sci. Rep.* 2, 804. doi:10.1038/srep00804.

Glynn, P. W. (1973). “Aspects of the ecology of coral reefs in the western Atlantic region,”

- in *Biology and Geology of Coral Reefs, Vol. 2*, eds. O. A. Jones and R. Endean (New York: Academic Press), 271–324.
- Griffin, J. N., Schrack, E. C., Lewis, K.-A., Baums, I. B., Soomdat, N., and Silliman, B. R. (2015). Density-dependent effects on initial growth of a branching coral under restoration. *Restor. Ecol.*, 1–4. doi:10.1111/rec.12173.
- Hixon, M. A., and Webster, M. S. (2002). “Density dependence in reef fish populations,” in *Coral reef fishes: dynamics and diversity in a complex ecosystem* (San Deigo, CA: Academic Press), 303–325.
- Hixon, M., and Carr, M. (1997). Synergistic predation, density dependence, and population regulation in marine fish. *Science*. 277, 946–949.
- Hogarth, W. (2006). Endangered and Threatened Species: Final Listing Determinations for Elkhorn Coral and Staghorn Coral. *Fed. Regist.* 71, 26852–26872.
- Holbrook, S. J., Brooks, A. J., Schmitt, R. J., and Stewart, H. L. (2008). Effects of sheltering fish on growth of their host corals. *Mar. Biol.* 155, 521–530. doi:10.1007/s00227-008-1051-7.
- Holbrook, S. J., Forrester, G. E., Schmitt, R. J., Holbrook, S. J., Forrester, G. E., and Schmitt, R. J. (2000). Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122, 109–120.
- Holl, K., Loik, M., Lin, E., and Samuels, I. (2000). Tropical montane forest restoration in Costa Rica: overcoming barriers to dispersal and establishment. *Restor. Ecol.* 8, 339–349. doi:10.1046/j.1526-100x.2000.80049.x.
- Hothorn, T., Bretz, F., and Westfall, P. (2008). Simultaneous inference in general parametric models. *Biometrical J.* 50, 346–363.

- Houlbrèque, F., and Ferrier-Pagès, C. (2009). Heterotrophy in tropical scleractinian corals. *Biol. Rev.* 84, 1–17. doi:10.1111/j.1469-185X.2008.00058.x.
- Hughes, T. (1994). Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science*. 265, 1547–1551.
- Jackson, J. B. C., Donovan, M. K., Cramer, K. L., and Lam, W. (2014). *Status and Trends of Caribbean Coral Reefs : 1970-2012*. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.
- Johnston, L., and Miller, M. W. (2014). Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs* 33, 1047–1056. doi:10.1007/s00338-014-1176-8.
- Kerry, J. T., and Bellwood, D. R. (2015). Do tabular corals constitute keystone structures for fishes on coral reefs? *Coral Reefs* 34, 41–50. doi:10.1007/s00338-014-1232-4.
- Kiel, C., Huntington, B., and Miller, M. (2012). Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. *Endanger. Species Res.* 19, 171–176. doi:10.3354/esr00474.
- Ladd, M. C., and Shantz, A. A. (2016). Novel enemies – previously unknown predators of the bearded fireworm. *Front. Ecol. Environ.* 14, 342–343. doi:10.1002/fee.1305/supinfo.
- Lesser, M. P., Weis, V. M., Patterson, M. R., and Jokiel, P. L. (1994). Effects of morphology and water motion on carbon delivery and productivity in the reef coral, *Pocillopora damicornis* (Linnaeus): Diffusion barriers, inorganic carbon limitation, and biochemical plasticity. *J. Exp. Mar. Bio. Ecol.* 178, 153–179. doi:10.1016/0022-0981(94)90034-5.
- Li, X., and Wilson, S. D. (1998). Facilitation among woody plants establishing in an old field. *Ecology* 79, 2694–2705.

- Lirman, D. (1999). Reef fish communities associated with *Acropora palmata*: Relationships to benthic attributes. *Bull. Mar. Sci.* 65, 235–252.
- Lirman, D., Schopmeyer, S., Galvan, V., Drury, C., Baker, A. C., and Baums, I. B. (2014). Growth dynamics of the threatened Caribbean Staghorn Coral *Acropora cervicornis*: influence of host genotype, symbiont identity, colony size, and environmental setting. *PLoS One* 9, e107253. doi:10.1371/journal.pone.0107253.
- Marhaver, K., Vermeij, M., Rohwer, F., and Sandin, S. (2013). Janzen-Connell effects in a broadcast-spawning Caribbean coral: distance-dependent survival of larvae and settlers. *Ecology* 94, 146–160.
- Miller, A. C. (1981). Cnidarian prey of the snails *Coralliophila abbreviata* and *C. caribaeae* (Gastropoda-Muricidae) in Discovery Bay, Jamaica. *Bull. Mar. Sci.* 31, 932–934.
- Moberg, F., and Folke, C. (1999). Ecological goods and services of coral reef ecosystems. *Ecol. Econ.* 29, 215–233. doi:10.1016/S0921-8009(99)00009-9.
- Morgan, J. W., and Scacco, P. J. (2006). Planting designs in ecological restoration: Insights from the Button Wrinklewort. *Ecol. Manag. Restor.* 7, 51–54. doi:10.1111/j.1442-8903.2006.00248.x.
- Mulligan, M. K., Kirkman, L. K., and Mitchell, R. J. (2002). *Aristida beyrichiana* (Wiregrass) establishment and recruitment: implications for restoration. *Restor. Ecol.* 10, 68–76.
- Mumby, P. J., and Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol. Evol.* 23, 555–63. doi:10.1016/j.tree.2008.06.011.
- Newman, S. P., Meesters, E. H., Dryden, C. S., Williams, S. M., Sanchez, C., Mumby, P. J.,

- et al. (2015). Reef flattening effects on total richness and species responses in the Caribbean. *J. Anim. Ecol.* 84, 1678–1689. doi:10.1111/1365-2656.12429.
- Pandolfi, J. M. (2015). Incorporating uncertainty in predicting the future response of coral reefs to climate change. *Annu. Rev. Ecol. Evol. Syst.* 46, 281–303. doi:10.1146/annurev-ecolsys-120213-091811.
- Pendleton, L. H., Hoegh-Guldberg, O., Langdon, C., and Comte, A. (2016). Multiple stressors and ecological complexity require a new approach to coral reef research. *Front. Mar. Sci.* 3, 1–9. doi:10.3389/fmars.2016.00036.
- R Core Team (2013). R: A Language and Environment for Statistical Computing. Available at: <http://www.r-project.org/>.
- Reaka-Kudla, M. L. (2005). *Biodiversity of Caribbean Coral Reefs*.
- Rinkevich, B. (2014). Rebuilding coral reefs: does active reef restoration lead to sustainable reefs? *Curr. Opin. Environ. Sustain.* 7, 28–36. doi:10.1016/j.cosust.2013.11.018.
- Ruzicka, R., Colella, M., Porter, J., Morrison, J., Kidney, J., Brinkhuis, V., et al. (2013). Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Mar. Ecol. Prog. Ser.* 489, 125–141. doi:10.3354/meps10427.
- Schopmeyer, S. A., and Lirman, D. (2015). Occupation dynamics and impacts of damselfish territoriality on recovering populations of the threatened staghorn coral, *Acropora cervicornis*. *PLoS One* 10. doi:10.1371/journal.pone.0141302.
- Shaish, L., Levy, G., Katzir, G., and Rinkevich, B. (2010). Employing a highly fragmented, weedy coral species in reef restoration. *Ecol. Eng.* 36, 1424–1432. doi:10.1016/j.ecoleng.2010.06.022.
- Shantz, A. A., Ladd, M. C., Shrack, E., and Burkepile, D. E. (2015). Fish-derived nutrient

- hotspots shape coral reef benthic communities. *Ecol. Appl.* 25, 2142–2152.
doi:10.1890/14-2209.1.
- Shantz, A., and Burkepile, D. (2014). Context-dependent effects of nutrient loading on the coral-algal mutualism. *Ecology* 95, 1995–2005.
- Shantz, A., Stier, A., and Idjadi, J. A. (2011). Coral density and predation affect growth of a reef-building coral. *Coral Reefs* 30, 363–367. doi:10.1007/s00338-010-0694-2.
- Sleeman, J. C., Boggs, G. S., Radford, B. C., and Kendrick, G. A. (2005). Using agent-based models to aid reef restoration: Enhancing coral cover and topographic complexity through the spatial arrangement of coral transplants. *Restor. Ecol.* 13, 685–694.
doi:10.1111/j.1526-100X.2005.00087.x.
- Sussman, M., Loya, Y., Fine, M., and Rosenberg, E. (2003). The marine fireworm *Hermodice carunculata* is a winter reservoir and spring-summer vector for the coral-bleaching pathogen *Vibrio shiloi*. *Environ. Microbiol.* 5, 250–5.
- Szmant, A. (1986). Reproductive ecology of Caribbean reef corals. *Coral reefs* 5, 43–53.
- Towle, E. K., Enochs, I. C., and Langdon, C. (2015). Threatened Caribbean coral is able to mitigate the adverse effects of ocean acidification on calcification by increasing feeding rate. *PLoS One* 10, e0123394. doi:10.1371/journal.pone.0123394.
- Tunncliffe, V. (1981). Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc. Natl. Acad. Sci. U. S. A.* 78, 2427–2431. doi:10.1073/pnas.78.4.2427.
- Vollmer, S. V., and Kline, D. I. (2008). Natural disease resistance in threatened staghorn corals. *PLoS One* 3, e3718. doi:10.1371/journal.pone.0003718.
- Williams, D. E., and Miller, M. W. (2005). Coral disease outbreak: pattern, prevalence and transmission in *Acropora cervicornis*. *Mar. Ecol. Prog. Ser.* 301, 119–128.

Young, C., Schopmeyer, S., and Lirman, D. (2012). A Review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic.

Bull. Mar. Sci. 88, 1075–1098. doi:10.5343/bms.2011.1143.

Zahawi, A. R. A., and Augspurger, C. K. (2012). Tropical forest restoration: tree islands as recruitment foci in degraded lands of Honduras. *Ecol. Appl.* 16, 464–478.

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

With Andrew A. Shantz, Erich E. Bartels, and Deron E. Burkepile

Reprinted by permission from *Marine Ecology Progress Series*: Ladd, M.C., Shantz, A.S., Bartels, E.B., and Burkepile, D.E. 2017. Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*. *Marine Ecology Progress Series*. 572: 129-139.

A. Introduction

Coral reefs comprise the ecological, economic, and social backbone of tropical coastal communities worldwide (Burke et al. 2011). However, coral reefs are being lost at an alarming rate (Bruno & Selig 2007), particularly in the Caribbean where reefs have lost ca. 80% of their corals since the 1980's (Gardner *et al.* 2003; Jackson *et al.* 2014). To confront declines in coral cover, coral restoration, the process of outplanting nursery-raised corals to degraded reef sites, has become increasingly popular over the past decade (Young et al. 2012). However, coral restoration is time consuming, costly, and in some cases, restored corals meet the same fate as the coral predecessors they are intended to replace. Accordingly, research identifying the mechanisms that dictate restoration success or optimize restoration strategies is sorely needed. To date, studies have investigated the influence of a variety of factors on the growth and survival of restored corals including outplant size (Garrison & Ward 2008), density (Ladd et al. 2016), genotype (Lirman et al. 2014), source location (Forrester et al. 2013), and species diversity (Cabaitan et al. 2015). However, despite recent progress, significant knowledge gaps in our understanding of coral restoration remain that may impede our ability to successfully restore coral reef communities.

One important gap is understanding how the genotypic diversity and identity of corals used for restoration affect the outcome of restoration efforts. Genotypic diversity can impact ecosystem function via complementarity among genotypes in ecologically important traits, such as biomass production or disease resistance (Fargione *et al.* 2007; Hughes & Stachowicz 2011). Alternatively, one or several genotypes can outperform others in a particular trait and drive population level patterns (i.e., the sampling effect; Loreau & Hector 2001). For example, Reusch *et al.* (2005) documented 4-fold differences in shoot density

between restored seagrass (*Zostera marina*) genotypes when confronted with thermal stress. Indeed, *Z. marina* displays genotype-specific differences across ecologically important traits such as shoot biomass, production, and nutrient uptake (Hughes et al. 2009). Accordingly, genotypically diverse populations can better resist or recover from disease (Mundt 2002), species invasions (Crutsinger et al. 2008), herbivory (Peacock & Hunter 2001; Hughes & Stachowicz 2004), and environmental extremes (Reusch et al. 2005). Given the multitude of stressors influencing marine systems, environmental and biological context will likely influence intraspecific differences in important ecological traits. Thus, the differences in traits among genotypes may be an important driver of the impact of genotypic diversity in determining population performance. In the context of ecological restoration, genotype-specific traits may be especially important for choosing individuals that perform best or are robust to changes in environmental conditions in order to maximize restoration success.

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

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

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

B. Methods

Study Species

Acropora cervicornis is a fast-growing, branching coral species that can rapidly expand via asexual fragmentation (Glynn 1973; Tunnicliffe 1981). The structural complexity provided by *A. cervicornis* and its congener, *A. palmata*, provides essential habitat for a multitude of reef-associated organisms (Reviewed in Bruckner 2002). Historically, these two species were dominant habitat forming and reef-building species on many Caribbean reefs, including in the Florida Keys (Hughes 1994; Aronson & Precht 2001). Today, *A. cervicornis* populations on most Caribbean reefs have declined 80-90% compared to 1970's populations, with drastic population reductions of >95% in some areas (Hughes 1994; Aronson & Precht 2001; Bruckner 2002), resulting in significant losses in structural complexity on most Caribbean reefs and their listing as "Threatened" under the US Endangered Species Act (Hogarth 2006). Currently, coral restoration efforts are primarily focused on *A. cervicornis* due to its life history characteristics amenable to rapid propagation and the species' critical role on Caribbean coral reefs as habitat.

Experimental Design

Our field site was a low-relief reef in ~5-7m of water located approximately 10km offshore of Summerland Key, Florida, USA (24.532°N, 81.483°W). We established four experimental blocks of four 1m² plots ≥5m away from and parallel to the reef ledge. Each block of 1m² plots contained one replicate of each genotypic diversity treatment: 1-, 2-, 4-, or 6-genotypes. Within each block, 1m² plots were separated by 3-4m, while blocks of 1m² plots were separated by ~30m. Treatments were randomly assigned to plots within a block. Eight

genotypes (named D-K) were used to create experimental treatments. However, due to limited availability of certain genotypes, only four genotypes (D, E, F and G) were present in all treatment levels.

We outplanted twelve colonies of *A. cervicornis*, each approximately 35cm in total linear extension (TLE), to each plot in May of 2013 (Figure 1). We evenly spaced coral colonies within plots such that colony density and arrangement did not differ between treatments. We also organized colonies to maximize genotype mixing and avoid clumping of the same genotype in plots with multiple genotypes. Genotype analyses, completed as part of Mote Marine Laboratory's initial establishment of a coral nursery, were done using known microsatellite markers. Corals from confirmed genotypes had been grown in the Mote Marine Laboratory offshore coral nursery from 5-10cm fragments (E. Bartels, pers. comm.). We outplanted four replicates of each treatment in the randomized block design for a total of 192 corals outplanted into 16 1m² plots. Each colony was secured via a cable tie to a masonry nail hammered into the reef substrate and labeled with an individually numbered tag.

Coral Colony Growth, Condition and Predator Surveys

To quantify the effects of genotypic identity and diversity on colony growth, we measured coral colony dimensions (length, width and height) to the nearest centimeter every 3-6 months. Surveys were conducted in May, September, and December of 2013, June and October of 2014, and January of 2015. At each sampling event, we recorded the percent of each coral colony that had live tissue, presence of coral bleaching, and presence of disease via visual assessment. We also took a photograph of the entire plot from the same location to compare images through time. Additionally, we counted corallivorous snails (*Coralliophila*

abbreviata) and fireworms (*Hermodice carunculata*) on each *A. cervicornis* colony.

However, these predators were so rare that we did not explore these data quantitatively.

Beginning June 15, 2014, sea surface temperatures recorded at a site 9 km away at the same depth reached 30°C, just below the threshold for bleaching in *A. cervicornis* (Manzello et al. 2007). Temperatures at this site remained above 30°C from June 15 until October 7, 2014 (Appendix 4). During our June 2014 survey (June 19), we did not observe bleaching in any of our experimental *A. cervicornis* corals or naturally occurring coral colonies of any other species growing on the reef at our study site. Therefore, we refer to May 2013 through June 2014 as “pre-bleaching” surveys. During September and early October of 2014, >75% of *A. cervicornis* colonies observed in many areas of the Florida Keys exhibited some degree of bleaching (Manzello 2015). Although we were not able to sample our experiment during the regional height of the bleaching event, we did survey corals again on October 30, 2014. While the peak in bleaching at our study site is unknown, at this time corals still exhibited substantial bleaching and we therefore considered this our “bleaching” survey. Even though we may have missed the peak of the bleaching, the relative patterns in bleaching among genotypes were likely similar to the peak time of bleaching. Our final sampling was conducted in January 2015 for a “post-bleaching” survey, at which time bleached corals had died or recovered and no bleaching was observed.

Statistical Analyses

Total skeletal linear extension (TLE) was calculated using length, width, and height conversions provided by Kiel et al. (2012). Growth rates were calculated for each interval by dividing the TLE accumulated between survey periods by the number of days elapsed to

generate a daily growth rate. For all growth rate and TLE calculations, data for corals were not included if they showed signs of breakage that would confound actual coral growth rates. Corals that suffered 100% tissue loss were included in growth rate and TLE calculations for the first survey where total mortality was recorded, but were removed from future growth calculations to avoid artificially depressing growth rates or TLE measures by continually including dead corals in our calculations. Coral colonies were likely broken during natural processes such as turtle and fish activity within plots (M. Ladd, pers. obs.).

We assessed changes through time in growth rates, total linear extension, and percent of colony with no live tissue via nested two-way repeated measures ANOVAs. Genotypic diversity treatment effects were tested using plot as a replicate by calculating a mean value for the response variable of interest (growth rate, TLE, or percent of colony with no live tissue) for each plot. Treatment effect models considered treatment, survey and block as fixed factors with an interaction between treatment and survey and plot considered a random effect.

In separate models, we tested the effect of genotype on individual colony growth rate, TLE, and percent of colony with no live tissue, using a model that considered genotype, survey and block as fixed factors and included an interaction between genotype and survey. We did not include genotypic diversity treatment in this model because only a subset of genotypes were present in each treatment making it impossible to test for effects of both genotypic diversity and genotypic identity in the same model. In models testing for effects of genotype, individual corals were nested within a plot and considered as a random effect to avoid violating assumptions of independence. When there were significant genotypic diversity or genotype effects, we tested for differences among treatment or genotype for

individual survey periods via *post hoc* tests with Tukey's corrections using the *multcomp* package in R (Hothorn et al. 2008). Among genotype differences in percent of colony bleached were assed via an ANOVA using the October 2014 survey period. Growth rates, percent of colony with no live coral tissue, and percent of colony bleached were square-root transformed to meet ANOVA assumptions.

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

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

after our December 2013 survey (Figure 1). All analyses were conducted in R version 3.0.2 (R Core Team 2013).

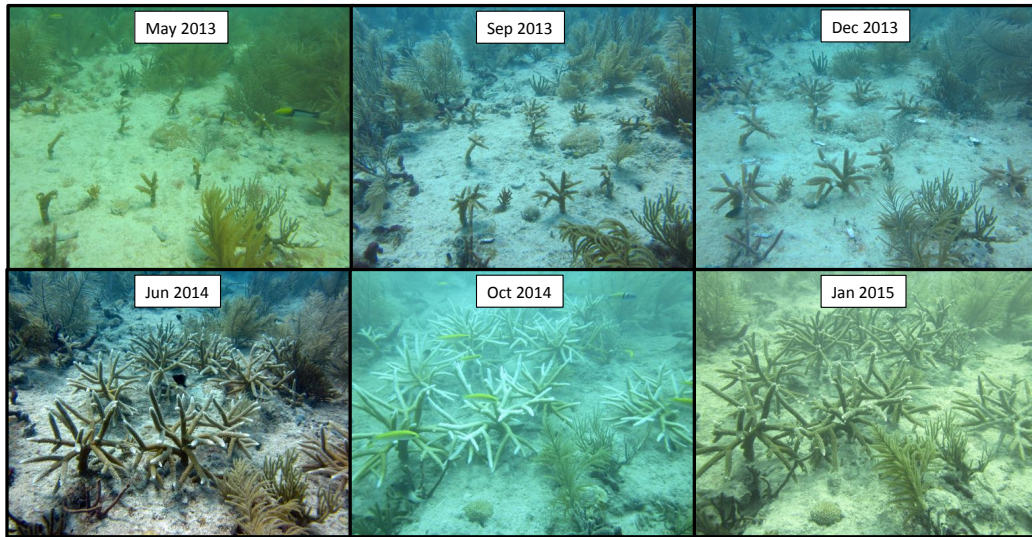


Figure 1. Photographic time series of an experimental plot during each survey periods. Evidence of bleaching and post-bleaching recovery is evident in October 2014 and January 2015.

C. Results

Genotypic Diversity Effects

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

	Response Variable	Predictor	df1	df2	F	P
Genotypic diversity effects	Growth rate (cm day ⁻¹)	Survey	5	59	27.15	< 0.001
		Treatment	3	9	0.25	0.86
		Treatment x Survey	15	59	0.71	0.77
		Block	3	9	0.1.77	0.22
	Total linear extension	Survey	5	59	38.55	< 0.001
		Treatment	3	9	0.30	0.82
		Treatment x Survey	15	59	0.34	0.99
		Block	3	9	1.27	0.34
	Percent of colony without live tissue	Survey	5	47	29.02	< 0.001
		Treatment	3	9	0.52	0.68
		Treatment x Survey	15	47	0.28	0.99
		Block	3	9	0.69	0.58
Genotype effects	Growth rate (cm day ⁻¹)	Survey	5	642	340.78	< 0.001
		Genotype	7	169	0.63	0.73
		Genotype x Survey	35	642	2.26	< 0.001
		Block	3	12	2.67	0.09
	Total linear extension	Survey	5	585	700.51	< 0.001
		Genotype	7	169	2.35	0.026
		Genotype x Survey	35	585	4.99	< 0.001
		Block	3	12	3.47	0.06
	Percent of colony without live tissue	Survey	5	905	276.16	< 0.001
		Genotype	7	169	6.21	< 0.001
		Genotype x Survey	35	905	5.75	< 0.001
		Block	3	12	0.62	0.61

Table 1. Results from nested two-way repeated measures ANOVA testing the effect of genotypic diversity treatment on growth rate, total linear extension, and percent of colony without live tissue and nested two-way repeated measures ANOVA testing the effect of genotype on mean growth rate, total linear extension, and percent of colony without live tissue.

Genotype Effects

Mean growth rates among genotypes ranged 4-fold, from a minimum of 0.18 to a maximum of 0.73 cm day⁻¹ (mean ±SE; 0.33 ±0.01) and significantly differed through time among genotypes (Genotype x Survey effect: $F_{35, 642} = 2.256$, $p < 0.001$; Figure 2a). However, *post-hoc* tests with Tukey's correction were unable to detect significant differences in growth rates among genotypes, likely due to the high number of comparisons conducted. Mean daily growth rates for genotype D nearly tripled after the 2014 thermal stress event (from 0.25 cm day⁻¹ to 0.73 cm day⁻¹), and manifested in a large increase in mean total linear extension (TLE), a proxy for habitat produced (Genotype x Survey effect: $F_{35,585} = 4.998$, $p <$

0.001; Figure 2b). We found that individuals of genotype D were on average 20-327% larger than the other genotypes by the end of the experiment.

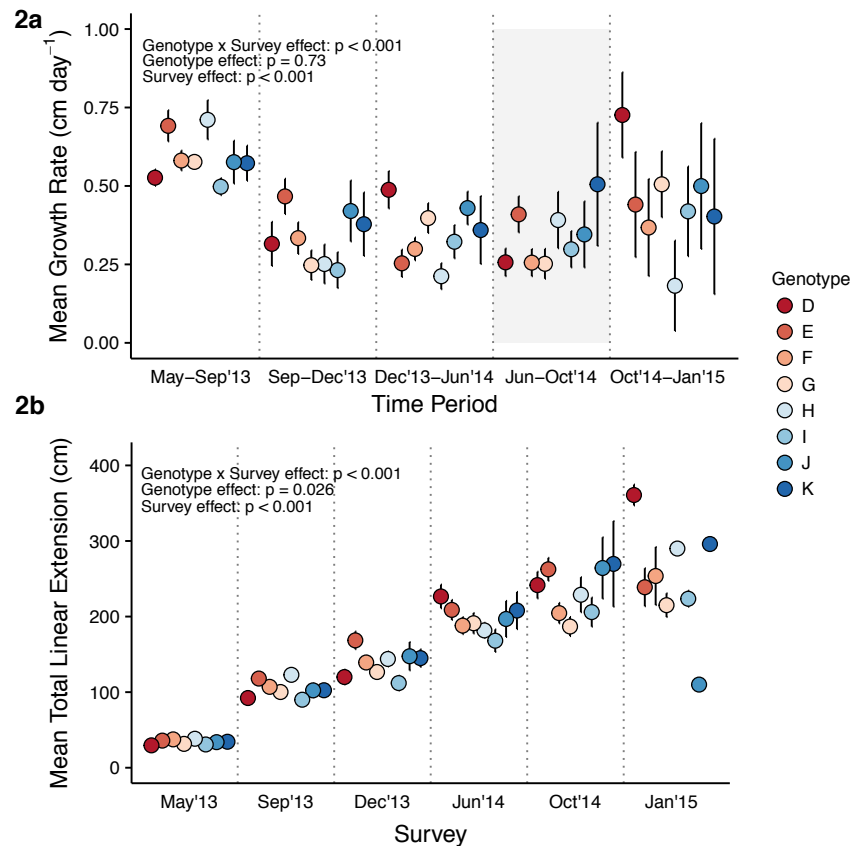


Figure 2. (a) Daily growth rate of individual genotypes through time regardless of treatment. Labels on the x-axis indicate the time period over which the growth rate was calculated. (b) Total linear extension of colonies by genotype throughout the experiment. Labels on the x-axis indicate the survey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

In 2014 a thermal stress event occurred from June 15 to October 7, during which sea surface temperatures near our study site remained above 30°C and caused significant bleaching and mortality in coral colonies throughout the Florida Keys (Manzello 2015). During our October 2014 survey, we observed significant differences among genotypes in the percent of coral colonies bleached ($F_{7,166} = 4.77$, $p < 0.001$; Figure 3). Specifically, genotype D and K corals had on average nearly twice the amount of bleached coral tissue per colony compared to all other genotypes.

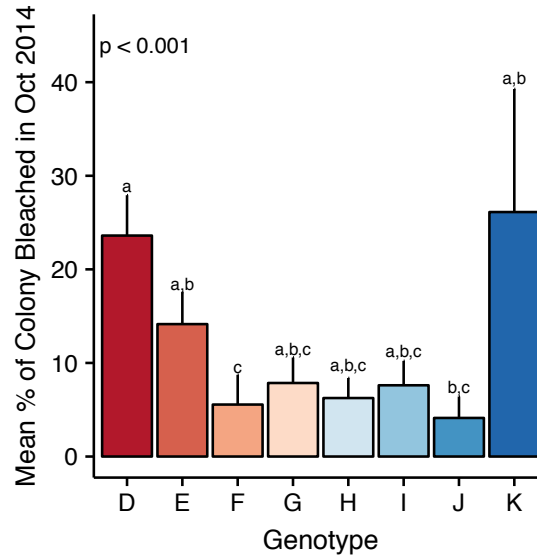


Figure 3. Mean percent of colony bleached in October 2014 for the eight *Acropora cervicornis* genotypes used in this study. Statistics are from one-way ANOVA. Different letters represent significant differences ($p < 0.05$) among genotypes from *post hoc* tests with Tukey's correction.

Genotypic differences in response to the thermal stress event were evident in cumulative survivorship, which varied 3-fold among genotypes (Fisher's Exact Test, $p < 0.001$; Figure 4a) and ranged from a high of 93.1% to a low of 27.8% colonies alive at the end of the experiment. There was no effect of genotypic diversity treatment on cumulative survivorship (Treatment effect: $F_{3,9} = 0.06$, $p = 0.98$). Thermal stress appeared to drive differences between genotypes in the average percent of a colony with no live tissue at the end of the experiment (Genotype x Survey effect: $F_{35,905} = 5.75$, $p < 0.001$; Figure 4b). By October 2014, genotypes E, F and J had lost live tissue on approximately 3x more of the skeleton per colony compared to genotypes D, G and I. This pattern held until the end of the experiment, suggesting there was little tissue recovery after the bleaching event for these genotypes. All results from nested two-way repeated measures ANOVAs can be found in Table 1.

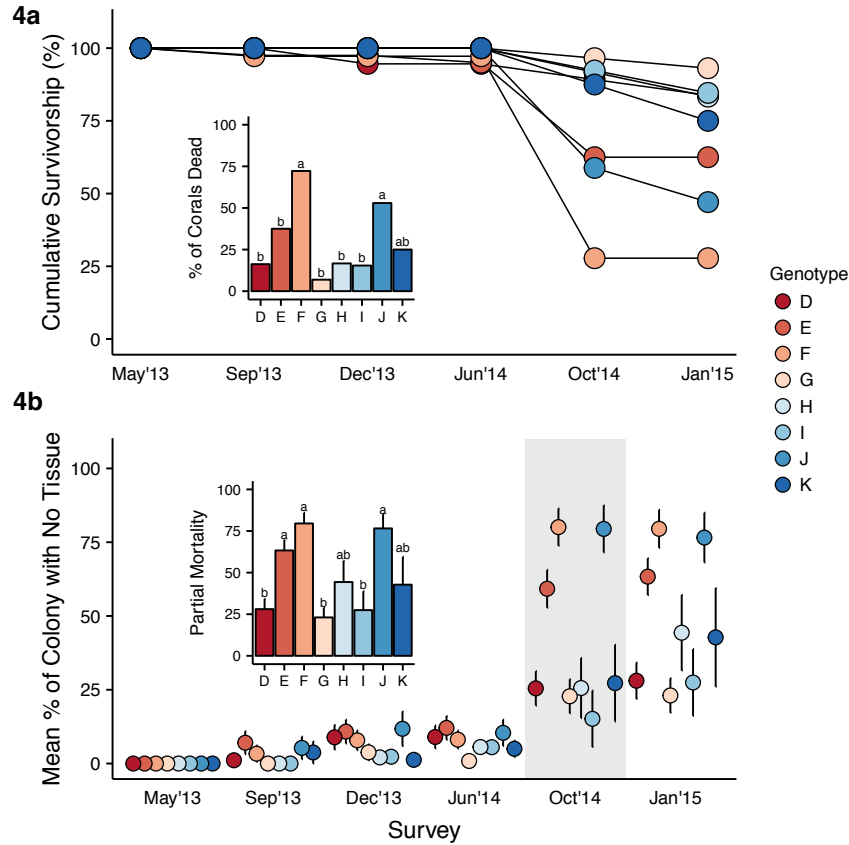


Figure 4. (a) Cumulative survivorship of colonies of the eight *Acropora cervicornis* genotypes used in this study. The inset bar plot presents the percent of corals dead for each genotype at the conclusion of the experiment. Different letters represent significant differences ($p < 0.05$) from Fisher's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

We found no relationship between mean initial growth rates (September to December 2013) and final TLE ($F_{1,6} = 0.513$, $p = 0.54$) across genotypes (Figure 5a). Thus, initial growth rates were not related to final amount of habitat created. Similarly, there was no relationship between initial growth rates and the amount of bleached tissue in coral colonies ($F_{1,6} = 0.417$, $p = 0.542$). However, the percent of tissue on a colony that died during the experiment was significantly positively related to initial genotype-specific growth rates ($F_{1,6}$

= 6.445, $p = 0.044$; Figure 5b), indicating that genotypes with faster initial growth rates ultimately lost more live tissue.

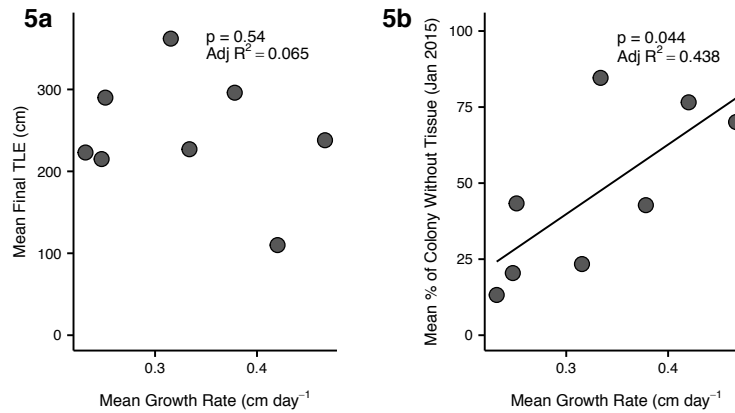


Figure 5. Average growth rate cm day^{-1} for each genotype from October to December 2013 regressed against (a) the mean TLE for each genotype and (b) mean percent of colony with no live tissue at the end of the experiment in January 2015. Statistics are from linear regression.

D. Discussion

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

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

One of the major goals of coral reef restoration is to restore ecological processes and feedbacks that can drive community recovery. One key driver of these positive feedbacks on reefs is the creation of structural complexity by live coral (Mumby & Steneck 2008), which provides habitat for diverse and ecologically important fish and invertebrate assemblages (Newman et al. 2015), refuge from predators (Almany 2004), and facilitates nutrient cycling (Holbrook et al. 2011; Shantz et al. 2015). Surprisingly, we found no relationship between initial growth rates and the amount of habitat produced by a coral. This finding suggests that

initial growth rates, often used to evaluate corals raised in nurseries (e.g. Griffin et al. 2012; Lirman et al. 2014), may not be a reliable predictor for how corals will perform when outplanted for restoration. Further, coral genotypes with initially high growth rates ended up losing more live tissue after the thermal stress event than colonies with slower initial growth rates, suggesting a tradeoff between growth rate and ability to cope with thermal stress. Another potential explanation for this tradeoff could be differences in energy allocation strategies between coral genotypes. Coral energy reserves are positively correlated with survival and recovery from bleaching events (Grottoli *et al.* 2014; Schoepf *et al.* 2015). However, calcification is an energetically intensive process. Thus, genotypes that devote more energy to rapid growth may possess smaller energy reserves than slower growing genotypes resulting in less capacity to deal with stressors.

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

Corals can exhibit high levels of local adaptation, including the ability to cope with a variety of stressful conditions (Barshis et al. 2010; Sanford & Kelly 2011). Such differences

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

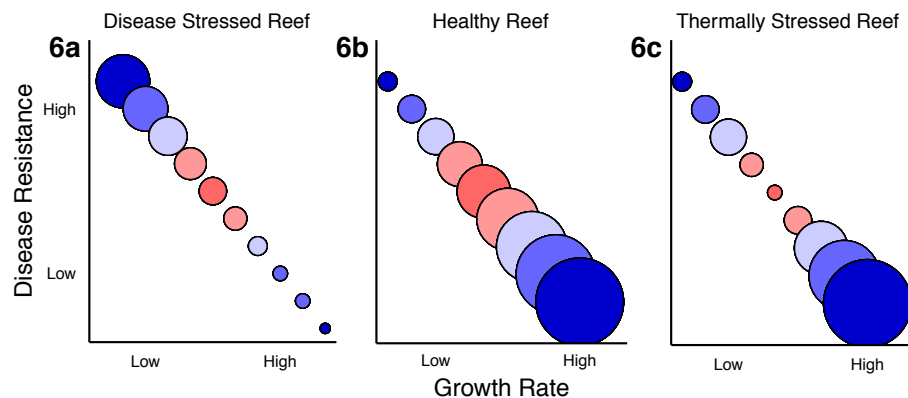


Figure 6. Visualization of a potential tradeoff among multiple coral traits under different environmental contexts. Each circle represents a distinct coral genotype. Cooler colors represent more thermally tolerant genotypes, while hotter colors represent thermally intolerant genotypes. The amount of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

Genotypic diversity of foundation species can be a major driver of community structure and ecosystem function (Crutsinger et al. 2006). However, we found that genotypic diversity had no effect on the growth rate, size, or survivorship of restored *A. cervicornis*. The unexpected lack of a genotypic diversity effect on restored coral performance may have been due to several factors. Restricted availability of specific genotypes limited our highest genotypic diversity treatment to six genotypes, while genotypic diversity effects may be evident only at higher levels of genotypic diversity. However, the prominence of asexual fragmentation by *A. cervicornis* (Tunnickliffe 1981) and extremely low sexual recruitment in the Florida Keys (van Woesik et al. 2014) suggest that our genotypic diversity treatments were within realistic ranges for natural populations. Diversity effects may be emergent properties only evident at the level of ecosystem processes such as primary production or nutrient cycling and not detectable by measuring growth and survivorship responses in individual corals. Alternatively, specific genotype combinations may be required to generate hypothesized genotypic diversity effects. For example, in rocky intertidal seaweed communities, biodiversity can enhance nitrate uptake and photosynthesis, but only in realistic (non-random) assemblages (Bracken & Williams 2013). Thus, it is plausible that genotypic composition of restored coral populations is as important, if not more, than genotypic diversity for restoration success.

The need for coral restoration is becoming increasingly urgent as the worlds' reefs continue to lose corals (De'ath et al. 2012; Jackson et al. 2014; Graham et al. 2015; Hughes et al. 2017). It is critical to recognize that environmental conditions are variable across reefs and over space and time. Thus, matching genotype-specific performance to the environmental conditions of restoration sites will be critical to furthering restoration goals.

We suggest weighting restoration at sites with predictable conditions towards genotypes with known attributes that can boost survivorship and habitat production. Conversely, at sites prone to frequent disturbances or highly variable conditions, including a suite of traits from numerous genotypes at a single restoration site may be important to maximize the likelihood that these populations will persist under uncertain future conditions (Pandolfi 2015; Pendleton *et al.* 2016). Ultimately, long term studies assessing how different genotypes perform under a variety of environmental conditions will afford restoration practitioners the ability to select genotypes best suited for site-specific conditions and increase the chances of achieving restoration goals.

E. Acknowledgments

This work was conducted under permit FKNMS-2011-150-A2 and facilitated by a grant from the National Science Foundation, Biological Oceanography program (OCE-1130786) to DEB. We thank Mote Marine Laboratory for providing the *Acropora cervicornis* colonies, boat time, and fieldwork assistance. We thank C. Walter, E. Shaver, C. Fuchs, and S. Csik for assistance in the field, N. Lemoine for guidance on statistical analyses, and two anonymous reviewers for comments that improved the manuscript.

F. References

- Almany GR (2004) Differential effects of habitat complexity, predators and competitors on abundance of juvenile and adult coral reef fishes. *Oecologia* 141:105–113
- Aronson R, Precht W (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38

- Barshis DJ, Stillman JH, Gates RD, Toonen RJ, Smith LW, Birkeland C (2010) Protein expression and genetic structure of the coral *Porites lobata* in an environmentally extreme Samoan back reef: does host genotype limit phenotypic plasticity? *Mol Ecol* 19:1705–20
- Baums IB (2008) A restoration genetics guide for coral reef conservation. *Mol Ecol* 17:2796–811
- Bowden-Kerby A (2008) Restoration of threatened *Acropora cervicornis* corals: intraspecific variation as a factor in mortality, growth, and self-attachment. In: Proceedings of the 11th International Coral Reef Symposium. p 1194–1198
- Bracken MES, Williams SL (2013) Realistic changes in seaweed biodiversity affect multiple ecosystem functions on a rocky shore. *Ecology* 94:1944–1954
- Bruckner AW (2002) Proceedings of the Caribbean *Acropora* Workshop: Potential Application of the U.S. Endangered Species Act as a Conservation Strategy. Silver Spring, MD
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PLoS One* 2:e711
- Burke L, Reytar K, Spalding M, Perry A (2011) *Reefs at Risk Revisited*.
- Cabaitan PC, Yap HT, Gomez ED (2015) Performance of single versus mixed coral species for transplantation to restore degraded reefs. *Restor Ecol* 23:1–8
- Chadwick NE, Morrow KM (2011) Competition Among Sessile Organisms on Coral Reefs. In: Dubinsky Z, Stambler N (eds) *Coral Reefs: An Ecosystem in Transition*. Springer Netherlands, Dordrecht, p 347–371
- Crutsinger GM, Collins MD, Fordyce JA, Gompert Z, Nice CC, Sanders NJ (2006) Plant

genotypic diversity predicts community structure and governs an ecosystem process.

Science (80-) 313:966–968

Crutsinger GM, Souza L, Sanders NJ (2008) Intraspecific diversity and dominant genotypes resist plant invasions. *Ecol Lett* 11:16–23

De'ath G, Fabricius KE, Sweatman H, Puotinen M (2012) The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci* 109:17995–17999

Descombes P, Wisz MS, Leprieur F, Parravicini V, Heine C, Olsen SM, Swingedouw D, Kulbicki M, Mouillot D, Pellissier L (2015) Forecasted coral reef decline in marine biodiversity hotspots under climate change. *Glob Chang Biol* 21:2479–2487

Forrester GE, Taylor K, Schofield S, Maynard A (2013) Colony growth of corals transplanted for restoration depends on their site of origin and environmental factors. *Mar Ecol* 34:186–192

Gardner T, Côté I, Gill J, Grant A, Watkinson A (2003) Long-term region-wide declines in Caribbean corals. *Science* 301:958–960

Garrison V, Ward G (2008) Storm-generated coral fragments: A viable source of transplants for reef rehabilitation. *Biol Conserv* 141:3089–3100

Gattuso J-P, Magnan A, Bille R, Cheung WWL, Howes EL, Joos F, Allemand D, Bopp L, Cooley SR, Eakin CM, Hoegh-Guldberg O, Kelly RP, Portner H-O, Rogers AD, Baxter JM, Laffoley D, Osborn D, Rankovic A, Rochette J, Sumaila UR, Treyer S, Turley C (2015) Contrasting futures for ocean and society from different anthropogenic CO₂ emissions scenarios. *Science* 349:aac4722

Glynn PW (1973) Aspects of the ecology of coral reefs in the western Atlantic region. In: Jones OA, Endean R (eds) *Biology and Geology of Coral Reefs*, Vol. 2. Academic

Press, New York, p 271–324

- Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:1–17
- Griffin S, Spathias H, Moore T (2012) Scaling up *Acropora* nurseries in the Caribbean and improving techniques. *Proc 12th Int Coral Reef Symp*:9–13
- Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, Mcginley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob Chang Biol* 20:3823–3833
- Hoegh-Guldberg O, Mumby PJ, Hooten A, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatzioiols ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–42
- Hogarth W (2006) Endangered and Threatened Species: Final Listing Determinations for Elkhorn Coral and Staghorn Coral. *Fed Regist* 71:26852–26872
- Holbrook SJ, Schmitt RJ, Brooks AJ (2011) Indirect effects of species interactions on habitat provisioning. *Oecologia* 166:739–749
- Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical J* 50:346–363
- Hughes T (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 265:1547–1551
- Hughes AR, Stachowicz JJ (2004) Genetic diversity enhances the resistance of a seagrass ecosystem to disturbance. *Proc Natl Acad Sci* 101:8998–9002
- Hughes AR, Stachowicz JJ, Williams SL (2009) Morphological and physiological variation

- among seagrass (*Zostera marina*) genotypes. *Oecologia* 159:725–733
- Hughes AR, Stachowicz JJ (2011) Seagrass genotypic diversity increases disturbance response via complementarity and dominance. *J Ecol* 99:445–453
- Hughes TP, Kerry J, Álvarez-Noriega M, Álvarez-Romero J, Anderson K, Baird A, Babcock R, Beger M, Bellwood D, Berkelmans R et al. (2017) Global warming and recurrent mass bleaching of corals. *Nature* doi:10.1038/nature21707
- Jackson JBC, Donovan MK, Cramer KL, Lam W (2014) Status and Trends of Caribbean Coral Reefs: 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland
- Jin YK, Lundgren P, Lutz A, Raina J-B, Howells EJ, Paley AS, Willis BL, Oppen M van (2016) Genetic markers for antioxidant capacity in a reef-building coral. *Sci Adv* 2:e1500842
- Kiel C, Huntington B, Miller M (2012) Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. *Endanger Species Res* 19:171–176
- Ladd MC, Shantz AA, Nedimyer K, Burkepile DE (2016) Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Front Mar Sci* 3:1–14
- Lirman D, Schopmeyer S, Galvan V, Drury C, Baker AC, Baums IB (2014) Growth dynamics of the threatened Caribbean Staghorn Coral *Acropora cervicornis*: influence of host genotype, symbiont identity, colony size, and environmental setting. *PLoS One* 9:e107253
- Loreau M, Hector A (2001) Partitioning selection and complementarity in biodiversity experiments. *Nature* 412:72–76

- Manzello DP (2015) Rapid recent warming of coral reefs in the Florida Keys. *Sci Rep* 5:16762
- Manzello DP, Berkelmans R, Hendee JC (2007) Coral bleaching indices and thresholds for the Florida Reef Tract, Bahamas, and St. Croix, US Virgin Islands. *Mar Pollut Bull* 54:1923–1931
- Montoya-Maya PH, Smit KP, Burt AJ, Frias-Torres S (2016) Large-scale coral reef restoration could assist natural recovery: a case study in Seychelles, Indian Ocean. *Nat Conserv* 17:1–17
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol* 23:555–63
- Mundt CC (2002) Use of multiline cultivars and cultivar mixtures for disease management. *Annu Rev Phytopathol* 40:381–410
- Newman SP, Meesters EH, Dryden CS, Williams SM, Sanchez C, Mumby PJ, Polunin NVC (2015) Reef flattening effects on total richness and species responses in the Caribbean. *J Anim Ecol* 84:1678–1689
- Palmer C V, Bythell JC, Willis BL (2010) Levels of immunity parameters underpin bleaching and disease susceptibility of reef corals. *FASEB J* 24:1935–1946
- Pandolfi JM (2015) Incorporating uncertainty in predicting the future response of coral reefs to climate change. *Annu Rev Ecol Evol Syst* 46:281–303
- Peacock L, Hunter T (2001) Does host genotype diversity affect the distribution of insect and disease damage in willow cropping systems? *J Appl Ecol* 38:1070–1081
- Pendleton LH, Hoegh-Guldberg O, Langdon C, Comte A (2016) Multiple stressors and ecological complexity require a new approach to coral reef research. *Fron Mar Sci* 3:1–9

- R Core Team (2013) R: A Language and Environment for Statistical Computing.
- Reusch TB, Ehlers A, Hämmerli A, Worm B (2005) Ecosystem recovery after climatic extremes enhanced by genotypic diversity. *Proc Natl Acad Sci* 102:2826–2831
- Sanford E, Kelly MW (2011) Local adaptation in marine invertebrates. *Ann Rev Mar Sci* 3:509–35
- Schoepf V, Grottoli G, Levas SJ, Aschaffenburg D, Baumann JH, Matsui Y, Warner ME (2015) Annual coral bleaching and the long-term recovery capacity of coral. *Proc R Soc B Biol Sci* 282
- Shantz AA, Ladd MC, Shrack E, Burkepile DE (2015) Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecol Appl* 25:2142–2152
- Tunnicliffe V (1981) Breakage and propagation of the stony coral *Acropora cervicornis*. *Proc Natl Acad Sci U S A* 78:2427–2431
- Vollmer S V, Kline DI (2008) Natural disease resistance in threatened staghorn corals. *PLoS One* 3:e3718
- Woesik R van, Scott WJ, Aronson RB (2014) Lost opportunities: Coral recruitment does not translate to reef recovery in the Florida Keys. *Mar Pollut Bull* 88:110–117
- Young C, Schopmeyer S, Lirman D (2012) A Review of Reef Restoration and Coral Propagation Using the Threatened Genus *Acropora* in the Caribbean and Western Atlantic. *Bull Mar Sci* 88:1075–1098

III. Newly dominant benthic invertebrates reshape competitive networks on contemporary Caribbean reefs

With Andrew A. Shantz and Deron E. Burkepile

Reprinted by permission from Springer Nature: Ladd, M.C., Shantz, A.A, and Burkepile D.E.
2019. Newly dominant benthic invertebrates reshape competitive networks on contemporary
Caribbean reefs. *Coral Reefs*. 1-12

A. Introduction

Competition for limiting resources is a fundamental process that drives population dynamics, community succession, and structures ecological communities (Connell, 1961; Diamond, 1978; Barabás et al., 2016). On coral reefs, where space is often a limiting and highly contested resource, competition can be a major driver of benthic community composition (Connell, 1978; Lang and Chornesky, 1990; Connell and Hughes, 2004). When coral cover declines, as is occurring on reefs around the globe (Jackson et al., 2014; Hughes et al., 2018), the newly available substrate is often occupied by organisms that can rapidly colonize open space, such as macroalgae (Jackson et al., 2014; Graham et al., 2015). However, while coral-algal dynamics have justifiably received extensive research attention, algae are just one of many benthic groups that compete for space on coral reefs. Indeed, sponge and coral cover is now similar on many Caribbean reefs, with sponges actively overgrowing ~8-16% of corals on some reefs (Loh and Pawlik, 2014; Loh et al., 2015). Additionally, fast growing, “weedy” species such as hydrocorals, octocorals, gorgonians, and zoanthids have increased in abundance on Caribbean reefs (Burman et al., 2012; Ruzicka et al., 2013; Cruz et al., 2016). Consequently, the benthic communities of many contemporary Caribbean reefs are fundamentally different from historical assemblages (Aronson et al., 2004; Burman et al., 2012).

Shifts in ecological communities can generate novel interactions between species and alter interactive networks within a community (Gilman et al., 2010; Urban et al., 2012). Thus, there is a need to evaluate interactions among contemporary benthic invertebrates to understand how competition influences benthic community assemblages. Here, we present one of the first studies examining competitive interactions among a suite of sessile benthic

invertebrates representing a variety of taxa, growth strategies, and life history traits found on modern coral reefs.

The Florida Reef Tract has some of the lowest coral cover in the Caribbean (Gardner et al., 2003; Jackson et al., 2014), with many reefs now dominated by benthic invertebrates such as gorgonians and sponges (Ruzicka et al., 2013; Loh and Pawlik 2014). If coral reefs throughout the Caribbean continue to lose corals and experience shifts in community structure as predicted (Hoegh-Guldberg et al., 2007; Grottoli et al., 2014; Descombes et al., 2015), they may become similar in composition to present-day Florida reefs (Burman et al., 2012). Thus, research on Florida coral reefs provides important insights into how future Caribbean coral reefs may function. While there is a wealth of data on the benthic cover of Caribbean coral reefs and how communities have changed over recent decades, there is surprisingly little data quantifying interactions among benthic species (Chadwick and Morrow 2011), with most data focusing on coral-algal interactions (Swierts and Vermeij, 2016; but see Loh et al., 2015; Karlson, 1980).

To address these research gaps, we examined competitive interactions among historically abundant scleractinian corals on Caribbean reefs (*Orbicella faveolata* and *Acropora cervicornis*), corals increasing in relative abundance on contemporary reefs (*Siderastrea siderea* and *Porites porites*), and increasingly abundant non-scleractinian taxa, specifically fire corals, zoanthids, gorgonians, and sponges. We combined field surveys with a common garden competition experiment to investigate interference competition among these organisms, an important form of competition that can drive the presence and abundance of species (Jackson and Buss, 1975; Lang and Chornesky, 1990; Connell et al., 2004). Specifically, we addressed three main research questions: (1) What is the frequency of

interference competition among sessile benthic invertebrates on a contemporary Caribbean coral reef? (2) How do these species differ in aggressiveness (i.e., ability to reduce a competitor's live area) and susceptibility to competition (i.e., effect of competitors on their own growth rates)? And, (3) Does a competitive network exist among common sessile benthic invertebrates?

B. Materials and Methods

Study Species

We chose four scleractinian corals to comprise half of our focal species, representing a variety of life history strategies and varying historical and contemporary abundance on Caribbean reefs (Darling et al., 2012; Figure 1). *Orbicella faveolata* is a mounding, slow-growing species that has been historically abundant on Caribbean reefs (Gladfelter 1978). *Siderastrea siderea* is now one of the most abundant corals on reefs in Florida and the Caribbean (Burman et al., 2012; Perry et al., 2015) and exhibits a high tolerance to abiotic stressors such as temperature and sedimentation (Kemp et al., 2011). *Acropora cervicornis* is one of the fastest growing Caribbean coral species and was ubiquitous across Caribbean reefs before a massive die-off in the early 1980's (Aronson and Precht 2001). Currently, *Ac. cervicornis* is the primary species used in coral restoration efforts (Ladd et al., 2018). *Porites porites* is a branching coral relatively tolerant to a wide range of abiotic conditions and able to colonize disturbed habitats (Marcus and Thorhaug, 1981; Darling et al., 2012). Using ten species traits, Darling et al. (2012) classify these four coral species as employing distinct life history strategies: generalist (*O. faveolata*), stress-tolerant (*S. siderea*), competitive (*Ac. cervicornis*), and weedy (*P. porites*).

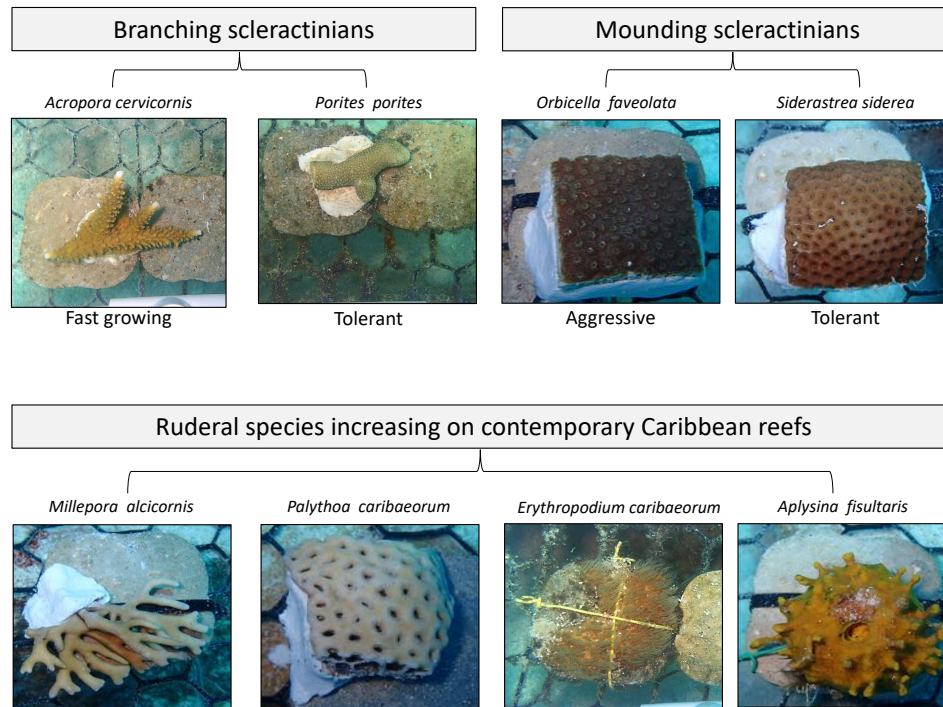


Figure 1. Photographs of the eight focal species used in this study affixed to experimental concrete pucks. Scleractinians (top row) are organized by morphology and prominent characteristics. Species on the bottom are representative of taxa increasing in abundance on Caribbean reefs and are generally characterized as aggressive, fast-growing, and ruderal species.

We also selected four non-scleractinian species that represent ruderal life-history strategies characteristic of groups that are increasingly common on Caribbean coral reefs (Knowlton 2001; Alvarez-Filip et al., 2011; Ruzicka et al., 2013). *Millepora alcicornis* is a fast growing, aggressive hydrocoral frequently observed overgrowing corals, gorgonians, and sponges (Wahle 1980; Wegener et al., 2018). *Erythropodium caribaeorum*, an encrusting gorgonian with inducible sweeper tentacles (Sebens and Miles 1988), and the zoanthid *Palythoa caribaeorum* are aggressive, fast-growing species (Bastidas and Bone 1996). Lastly, *Aplysina fistularis*, a common sponge species in Florida that produces biologically active metabolites (Walker et al., 1985). We chose these species to represent a broad range of sessile benthic invertebrates but note that extensive interspecific variation among important

traits exists within these groups and that these species are not necessarily representative of all related taxa.

Natural Competitive Interactions

To determine the abundance of our eight focal species and frequency of competitive interactions with other benthic invertebrates, we conducted photo transects at Pickles Reef (24.989°N, 80.376°W), a low-relief reef in 6-9 m of water 9 km offshore of Key Largo, Florida, USA in the Florida Keys National Marine Sanctuary (FKNMS). Along five 25 x 1 m haphazardly placed transects, we photographed 0.5 m x 0.5 m benthic quadrats (n = 50 quadrats per transect). From these photographs we identified all of the focal species present and classified the remaining non-focal invertebrates into one of three groups: “upright gorgonians”, “other sponges” (i.e. any sponge besides *Aplysina fistularis*), and “other hard corals” (i.e. any scleractinian other than the four focal species). Including these three additional groups allowed us to capture nearly all of the interactions among benthic invertebrates and thus better quantify the frequency of competitive interactions on the reef. For each benthic invertebrate observed in a photoquadrat, we recorded whether the individual was solitary or interacting with another individual and if interacting, recorded what species or group the individual was interacting with. We considered organisms to be interacting when any portion of another sessile benthic invertebrate was seen within 1 cm of the colony’s boundary. Although interference competition between corals can occur at distances >1 cm (Chadwick and Morrow 2011), distances at which many other benthic invertebrates can interact with neighbors is unknown. Therefore, to ensure that all individuals were actually interacting, we used 1 cm distance as a cutoff based on preliminary surveys that found

negative effects (e.g. altered growth, tissue paling, tissue mortality) between focal species at this distance. A single individual could be interacting with multiple other individuals. We considered an individual as a discrete unit with clear borders, thus nearby individuals of the same species could be fragments of the same genet. Shading and overtopping can be important forms of competition (Baird and Hughes 2000) but were not observed between our focal species and could not be accurately assessed from our top-down photographs. Thus, our estimates of interaction densities focus on interference competition and do not include mechanisms of exploitative competition like shading.

Although photographic transects allowed us to document the frequency of interference competition, it was difficult to quantify the outcome of these interactions from photographs. Instead, we conducted roving diver surveys to quantify the outcome of competitive interactions among the eight focal species. Roving diver surveys were conducted at Pickles Reef, Conch Reef (24.956°N, 80.458°W), and Pinnacles Reef (24.949°N, 80.503°W) in the Upper Florida Keys. For each survey, divers swam for 30 minutes away from a central point at predetermined headings to avoid censusing the same area. During each survey, we recorded every focal species we encountered that was interacting with another focal species and classified the outcome as one of three states, (1) win: individual had killed, damaged, or overgrown the competitor's tissue, identifiable by visible paling and mortality at the competition margin (Figure 2a) or the direct overgrowth of live tissue (Figure 2b); (2) loss: individual was killed, damaged, or overgrown by the competitor, or (3) draw: no signs of damage, tissue mortality, or overgrowth in either competitor (Figure 2c). We note these surveys represent a one-time snapshot of competitive interactions, and thus may not necessarily reflect the final outcome of the interaction (Wellington 1980; Chornesky 1989).

Common Garden Competition Experiment

To remove confounding factors and isolate spatial competitive ability, we conducted a competition experiment *in situ* using the eight focal species described above. In May 2014, we deployed 10 experimental platforms at 8-9 m depth on a sand flat near Pickles Reef. Each platform consisted of a 150 x 80 cm piece of PVC-coated wire mesh (2.5 cm diameter mesh size) secured to a PVC frame and placed on top of two cinderblocks (Appendix 5). A 1 m section of rebar was placed through the mesh on each corner and hammered into the sand to hold the platform in place and 20 cm tall mesh tops were secured to the platforms with cable ties to prevent fish predation on the focal species.

We obtained colonies of *O. faveolata* and *S. siderea* from the FKNMS Coral Nursery in Key West, Florida. Corals were transported to our field station in Key Largo in coolers filled with seawater, cut into 5 x 5 cm fragments using a tile saw, and transported immediately to our study site in fresh seawater. *Acropora cervicornis* fragments 5 cm in length were obtained from the Coral Restoration Foundation's underwater nursery in the upper Florida Keys, while similar sized *P. porites* fragments were collected from a nearby patch reef ~4 km away. All corals were transported directly to our field site after fragmentation and epoxied onto concrete pucks (5 x 5 x 0.5 cm) using underwater epoxy.

For our other focal species, we collected fragments of *M. alcicornis* (5 cm height, \leq 5 cm width), and colonies of *E. caribaeorum* (~5 x 5 cm), *P. caribaeorum* (~5 x 5 cm), and *Ap. fistularis* (\leq 5 cm diameter) from near Pickles Reef. We epoxied *M. alcicornis* to concrete pucks, and attached *Ap. fistularis*, *E. caribaeorum*, and *P. caribaeorum* to pucks via PVC coated wires, as these organisms had negative reactions to the fresh epoxy. All fragments

were collected and brought to the study site during the same seven-day period. Concrete pucks with experimental colonies were temporarily secured to the mesh tables at least 10 cm apart and allowed to acclimate for 14 days, at which time no colonies showed signs of mortality or fragmentation.

After acclimation, we rearranged fragments and paired them with either: a conspecific fragment from a different colony, another species, or an empty concrete puck that served as a control (n=5 per species for all possible combinations; Appendix 5). Concrete pucks were epoxied to the platforms such that competing organisms were in direct contact. Each competitive pair was separated from the nearest pair by 10 cm. Twenty-two pairs were arranged on every platform in a randomized block design so that all combinations were present on each set of platforms for a total of 220 experimental pairs. Mesh platforms and tops were brushed weekly to remove any fouling organisms.

On 18 July (initial time point), 23 October, and 11 December of 2014 (final time point) we took top-down photographs of each competitive pair and recorded any changes in colony appearance (e.g., paling), instances when an individual damaged or overgrew its competitor's tissue, and instances in which an individual killed, or was killed by its competitor. Finally, we analyzed each photograph in ImageJ® to measure colony area (cm²) and used these measurements to calculate the percent change in live area between the initial and final time points and the direction of growth for each individual (i.e., growing towards competitor, growing away from competitor, or no direction/unknown). Two-dimensional surface area is a common measure of growth and proxy for spatial competition, as it represents the amount of the limiting resource (i.e. space) a colony is using (Connell et al., 2004; Álvarez-Noriega et al., 2018).

Statistical Analysis

To calculate the percent cover of sessile invertebrates we overlaid a 50-point grid on each photoquadrat ($n = 50$ per transect) and used Coral Net (<https://coralnet.ucsd.edu>) to identify the substrate or organism below each point to the lowest taxonomic level possible. After identification, each point was categorized into one of 12 groups. Descriptions of these benthic groups and percent cover data are provided in Appendix 6. We used a linear mixed effects model with a binomial distribution to determine whether specific species or invertebrate groups had a higher probability of interacting with other benthic invertebrates. For this model, we included species (or invertebrate group) and percent cover as fixed interacting factors and transect as a random effect.

For the roving diver surveys, we analyzed whether each of the eight focal species was overgrowing (i.e. “winning”) or being overgrown (i.e. “losing”) by competitors more than expected by chance using a one-sample Wilcoxon signed rank test. For these two-sided tests, we assigned each of the three possible interaction outcomes a numeric value: win = 1, draw = 0, and loss = -1. We tested competitive outcomes observed for each species against the null hypothesis, $\mu = 0$ (draw), assuming that if a species was not competitively superior or inferior, there was an equal probability of an interaction ending in one of the three possible outcomes.

To measure the aggressiveness of each species in the common garden experiment, we calculated the mean percent change in live area of all heterospecific competitors when competing against that species. We did not include intraspecific competition for these analyses. We used two-sided t-tests to evaluate if the percent change in area that each species caused in their competitors’ area significantly differed from the average percent change in

the area of heterospecifics growing without competitors. To quantify each species' susceptibility to competition, we used two-sided t-tests to compare the mean change in area of a species when in competition with heterospecifics to the mean change in area of the conspecific controls.

To measure species-specific effects of spatial competition on growth, we calculated the change in percent live area relative to the mean change of that species without a competitor (i.e. controls) for each individual. We used the average change in live area for control individuals of each species to represent growth in the absence of a competitor due to variation among control replicates. We used the mean change in live area relative to control values to generate 95% confidence intervals using the 'summarySE' function in R for each species combination. For *O. faveolata*, we present data from July to October 2014 due to several control colonies exhibiting abnormally high levels of partial mortality from October to December 2014. We considered differences significant when the confidence interval did not overlap zero, with values lower than zero indicative of negative effects of competition with that particular species, while values above zero indicate a species performed better when in competition compared to control individuals (i.e. facilitation).

All analyses were conducted using R Version 3.4.3 (R Core Team 2017).

C. Results

Natural Competitive Interactions

Competition between benthic invertebrates was common, with 60% of the 3,267 individuals we recorded in our photoquadrats involved in an interaction. We found an average of 31 ± 2.8 interacting individuals m^{-2} (mean \pm SE) and 21 ± 0.69 solitary individuals

m⁻² organisms (Figure 2d; percent cover provided in Appendix 6). Upright gorgonians and *Ap. fistularis* were the most abundant benthic invertebrates observed (12.05 ±1.0 and 11.62 ±1.08 individuals m⁻², respectively). At low coral cover, both *Ap. fistularis* and *P. caribaeorum* had a higher probability of interacting than other invertebrate groups. Furthermore, as the percent cover of benthic invertebrates increased, the probability of interacting for *P. caribaeorum*, upright gorgonians, and other sponges grew significantly faster than other benthic invertebrate groups (Appendix 7). Approximately 85 ±5.4% of “other sponge” individuals (i.e. all sponges except *Ap. fistularis*) and 73 ±4.3% of *P. caribaeorum* colonies were interacting, the highest proportion for any species or groups we surveyed. In contrast, only 36 ±6.8% of “other hard corals” and 37 ±3.3% of *Porites porites* colonies surveyed were interacting with another benthic invertebrate. *Orbicella faveolata* and *Ac. cervicornis* were rare at this site and not observed on the transects.

Species	Lethal Interactions			Non-lethal Interactions			Growth Direction		
	Lost	Won	No Death	Tissue damaged by competitor	Damaged or overgrew competitors' tissue	No damage	Grew towards competitor	Grew away from competitor	No directional growth
<i>Acropora cervicornis</i>	27.9	4.7	67.4	4.7	11.6	83.7	39.5	2.3	58.2
<i>Aplysina fistularis</i>	0	2.3	97.7	6.8	52.3	49.9	61.4	11.4	27.2
<i>Erythropodium caribaeorum</i>	22.2	20.0	57.8	15.5	6.7	77.8	6.7	2.2	91.1
<i>Millepora alcicornis</i>	15.9	4.5	79.6	11.4	9.1	79.5	11.4	0	88.6
<i>Orbicella faveolata</i>	20.0	8.9	71.1	40.0	11.1	48.9	2.2	0	97.8
<i>Palythoa caribaeorum</i>	13.0	10.9	76.1	13.0	8.7	78.3	21.7	10.9	67.4
<i>Porites porites</i>	6.8	4.5	88.7	31.8	11.4	56.8	25.0	38.6	36.4
<i>Siderastrea siderea</i>	0	8.9	91.1	20.0	2.2	77.8	0	0	100

Table 1. Interaction outcomes from the common garden competition experiment. Lethal interactions: “Won” = individual killed its competitor, “Lost” = individual was killed by its competitor, “No Death” = neither competitor died. Non-lethal Interactions: “Tissue damaged by competitor” = individual’s tissue was damaged or overgrown by competitor, “Damaged or overgrew competitors’ tissue” = individual damaged or overgrew their competitor’s tissue, “No damage” = no damage or overgrowth by competitor. Growth Direction: “Grew towards competitor” = individual grew in the direction of competitor, “Grew away from competitor” = individual grew in a direction away from competitor, “No directional growth” = Individual did not grow or unable to determine the direction of growth. Data presented are the percent of all interactions for that species that resulted in a specific outcome.

From our roving diver surveys, we found several consistent patterns in competitive outcomes among the eight focal species surveyed. *Orbicella faveolata* and *Ap. fistularis* were observed winning the highest proportion of competitive interactions (83% and 71%, respectively; Figure 3). However, for *O. faveolata* this was not significantly different from the null hypothesis that wins, losses, and draws were equally probable ($p=0.13$), likely due to the rarity of this species in our surveys ($n=6$). In contrast, *Ap. fistularis* was abundant and found interacting with all seven other focal species. Interestingly, the only species that *Ap. fistularis* was not found overgrowing were *O. faveolata* and *Ac. cervicornis* (individual species outcomes are provided in Appendix 8). The third most successful species was *Ac. cervicornis*, which we found overgrowing competitors in 63% of observations. *Palythoa caribaeorum*, *E. caribaeorum*, and *M. alcicornis* were winning in approximately half of their interactions (54%, 51%, and 50%, respectively), but ranged widely in the percent of interactions lost (19.5 – 45%). The two remaining scleractinian corals, *P. porites* and *S. siderea*, were consistently being overgrown by their competitors, losing 76% and 92% of competitive interactions, respectively. Of all the interactions recorded for *P. porites* and *S. siderea*, the only instance of either species overgrowing a competitor was when they were interacting with each other (Appendix 8). Draws between species were the least common competitive outcome but were most frequent for *E. caribaeorum* (29% of interactions) and *P. caribaeorum* (19% of interactions).

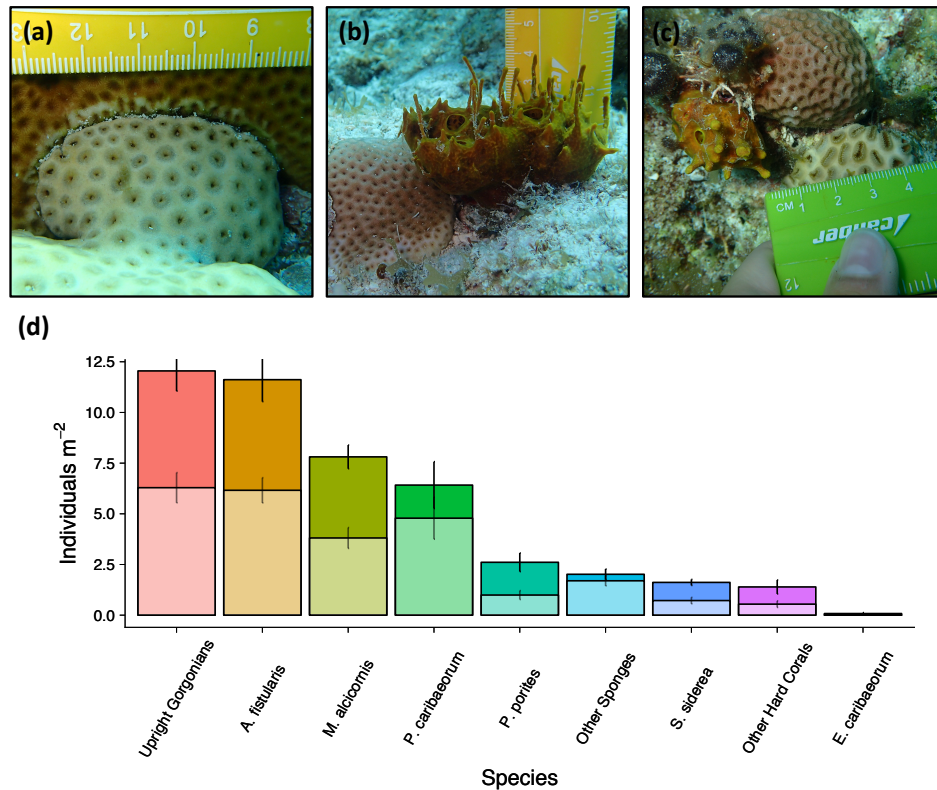


Figure 2. Photos of competitive interactions among common benthic invertebrates on contemporary reefs in the Florida Keys. (a) *Palythoa caribaeorum* killing the tissue of *Siderastrea siderea* (i.e. *P. caribaeorum* is “winning” and *S. siderea* is “losing”), (b) *Aplysina fistularis* overgrowing *S. siderea* (i.e. *Ap. fistularis* is “winning” and *S. siderea* is “losing”). (c) Standoff (i.e. “draw”) between *S. siderea* and *P. caribaeorum*. (d) Total density for each species or group recorded in field surveys represented by the tallest bars for each species or group. Lighter inset bars represent density of each species or group found interacting with another individual. For example, upright gorgonians had a density of 12.05 individuals m⁻² but only 6.3 individuals m⁻² were interacting with another individual. Data are means \pm SE.

Common Garden Competition Experiment

On average, four of the eight species reduced the live area of their competitors during the course of the experiment (Figure 4a). However, organisms differed widely in the amount they reduced their competitors’ live area. *Erythropodium caribaeorum* reduced competitors’ live area by $41.8 \pm 7.47\%$ while *O. faveolata* and *P. caribaeorum* reduced their competitors’ live area by $28.7\% \pm 6.04$ and $21.0\%, \pm 6.84$ respectively. The two weakest competitors in our natural interaction surveys, *S. siderea* and *P. porites*, were also two of the least aggressive of

our eight focal species (Figure 4a). While *Ap. fistularis* only outright killed its competitor in one instance during our common garden competition experiment, it was observed damaging or overgrowing its competitors' tissue 52% of the time, nearly 5x more often than any other of our focal species (Table 1). Further, *Ap. fistularis* was observed growing towards competitors in 61% of instances, in stark contrast to *P. porites* that grew away from competitors in ~39% of interactions.

Aggressiveness did not translate to increases in live area for most species. In fact, the four most aggressive species suffered the largest losses in live area, while less aggressive species gained live area or did not lose any area during the course of the experiment (Figure 4b). The most aggressive species, *E. caribaeorum*, lost >50% of their live area throughout the course of the experiment and were killed in 22% of interactions in our common garden experiment (Table 1). *Aplysina fistularis* was the only species where average growth was positive against all competitors, increasing in live area by $31.8 \pm 3.24\%$, though this was not different from the mean increase in area when paired with a control. Surprisingly, *P. porites*, one of the least aggressive species that was losing the majority of interactions in our field surveys, was the only other species that did not lose tissue area as a result of competition.

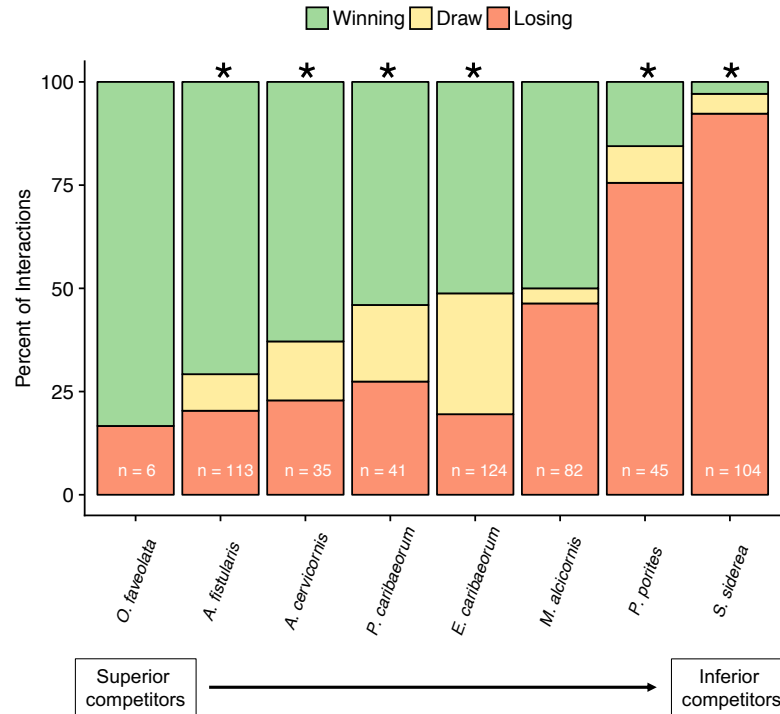


Figure 3. Competitive outcomes from field surveys in the summer of 2014 for the eight focal species of this study. Asterisks above bars denote that a species was found winning or losing significantly more interactions than predicted by the null model ($p < 0.05$; Wilcoxon test).

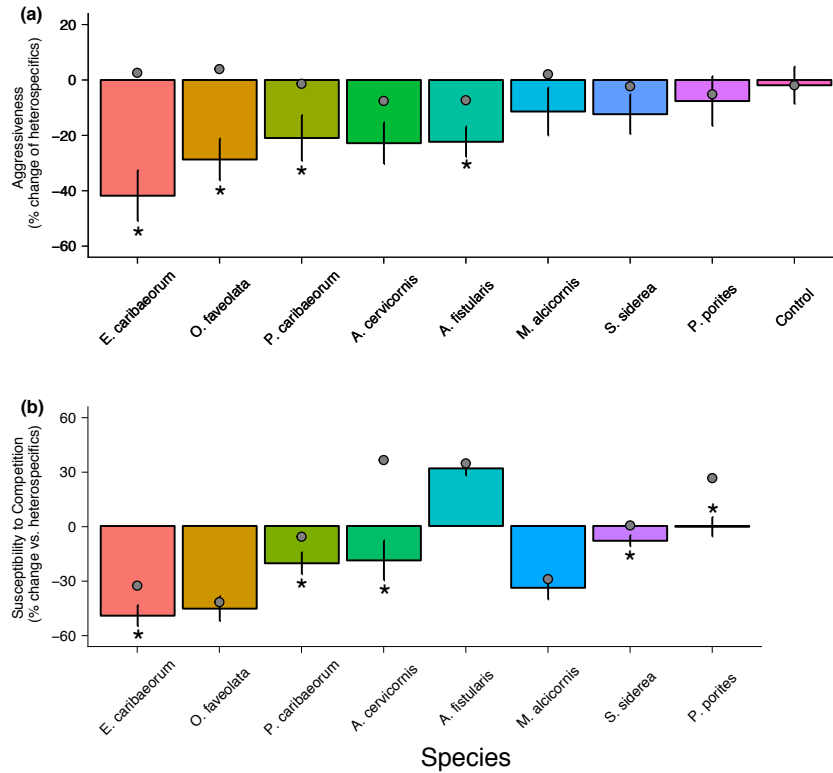


Figure 4. (a) Mean percent change in the live area of heterospecific competitors caused by each species from July to December 2014 (i.e. species aggressiveness). Gray points represent mean percent change in live area for heterospecifics when paired with controls. Data are means \pm SE from the common garden competition experiment. Asterisk indicates that the percent change in live area was significantly different from the mean percent change of heterospecific individuals when paired with controls ($p < 0.05$; two-sided t-test). (b) Mean percent change in the live area of each species in competition with all species (i.e. susceptibility to competition). Gray points represent mean percent change in live area for each species when paired with controls. Data are means \pm SE from the common garden competition experiment. Asterisk indicates that the percent change in live area was significantly different from mean percent change of that species when paired with controls ($p < 0.05$; two-sided t-test).

Species-specific interactions were largely similar to overall patterns in aggressiveness, with most species losing the most live area when competing against *E. caribaeorum*, *O. faveolata*, as well as conspecifics (Appendix 8). However, we also identified several nuanced interactions between species. For example, every *Ac. cervicornis* competing with *E. caribaeorum* was killed. Further, *M. alcicornis* growing in competition with *P. porites* grew significantly more than control fragments, suggesting a facilitative interaction may occur between these species that benefits *M. alcicornis*.

D. Discussion

On coral reefs, sessile organisms must compete for- and defend space on the benthos to successfully recruit, grow, and reproduce (Connell et al., 2004; Chadwick and Morrow 2011). The outcomes of these competitive interactions can shape benthic community assemblages, in turn influencing the quantity and quality of habitat available for a myriad of reef-associated organisms (Work et al., 2008; González-Rivero et al., 2011, 2016). Here, we found that competitive interactions were pervasive on Florida reefs, with 60% of sessile benthic invertebrates interacting with at least one other individual. At low invertebrate cover, *Ap. fistularis* and *P. caribaeorum* had the highest probability of being found interacting with other benthic invertebrates. Furthermore, the probability of being involved in an interaction increased more than predicted with increasing percent cover for *P. caribaeorum*, upright gorgonians, and other sponges, all of which employ a ruderal life history strategy. Our surveys and common garden competition experiment identified a non-transitive competitive network (Figure 5) as well as two species that were consistently inferior competitors. In our natural interaction surveys, *Ap. fistularis* and *Ac. cervicornis* won a higher proportion of their interactions than any other species except for the extremely rare coral *O. faveolata*. Importantly, *P. porites* and *S. siderea*, two of the most abundant scleractinians on contemporary Caribbean reefs (Burman et al., 2012; Perry et al., 2015), were consistently overgrown by all other focal species, suggesting that competition could limit the success of these species.

Interactions among benthic invertebrates were far more common than expected based on the amount of space they occupied for sponges (*Ap. fistularis* and other sponges), *P. caribaeorum*, and upright gorgonians. Several mechanisms could cause sessile invertebrates

to aggregate. First, when substrate becomes available non-invertebrate groups could rapidly expand, preempting suitable habitat for invertebrates to settle. At our site, turf-algal sediment matrix occupied >75% of the benthos. This consortium of short algal turfs can inhibit coral recruitment (Birrell et al., 2005), and thus may substantially reduce the substrate available for sessile invertebrates to colonize. Alternatively, aggregation could occur if multiple species utilize similar settlement cues. Regardless of the mechanisms responsible, the high frequency of interactions suggests that competition is a pervasive process influencing sessile invertebrates on Caribbean reefs, even when individual taxa are not especially abundant.

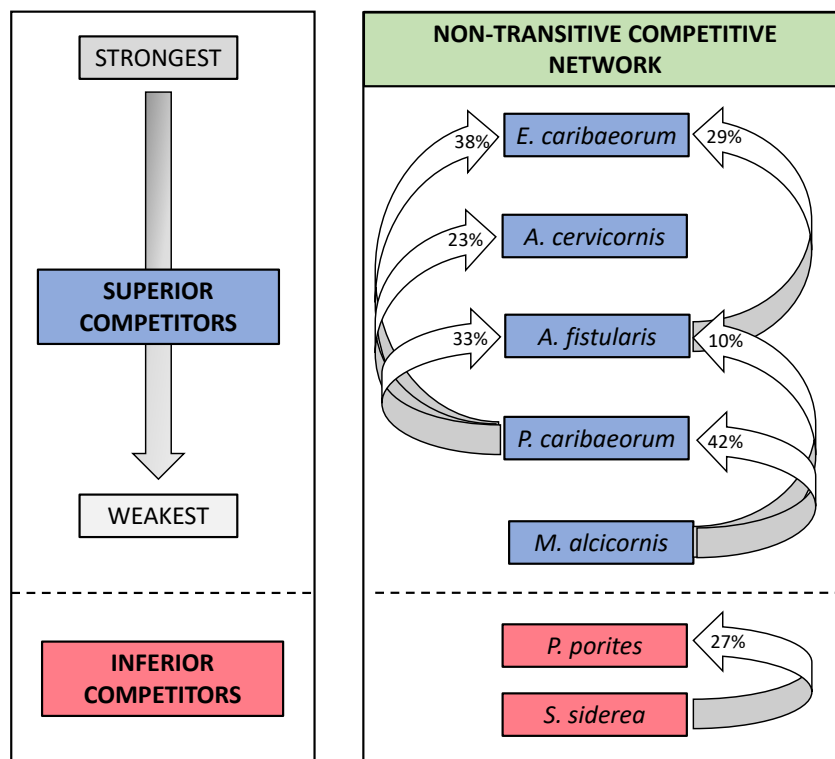


Figure 5. Non-transitive competitive network among seven of the eight focal species based on the outcomes of field surveys of competition and supported by results from the common garden competition experiment. Species at the top were observed winning the majority interactions with the species below them. Percentages in arrows represent the percent of interactions the inferior species was found winning against the superior competitor in natural interaction surveys (Appendix 8). *Orbicella faveolata* was not included due to being rare in our surveys.

While a substantial body of literature exists on intra- and interspecific competition among scleractinian corals (e.g. Lang, 1973; Lang and Chornesky, 1990; Chadwick and Morrow,

2011; Precoda et al., 2017; Álvarez-Noriega et al., 2018), there is a paucity of data on interactions between increasingly common benthic invertebrates and scleractinians. Our results from both natural and experimental interactions suggest that *P. porites* and *S. siderea* consistently lose aggressive interactions with other benthic invertebrates (Figure 5). In interactions between the other focal species, however, there were no clear superior competitors. For instance, *Ac. cervicornis* overgrew *Ap. fistularis* 100% of the time but had no winning interactions with *E. caribaeorum* (Appendix 8). However, *E. caribaeorum* in turn won less than half of its interactions with *Ap. fistularis*. This lack of a single dominant competitor is suggestive of a non-transitive network (*sensu* Buss and Jackson, 1979; Precoda et al., 2017), which can help maintain the diversity of competing community members. Thus, while there may not be a competitive dominant amongst these increasingly common benthic invertebrates, an increase in their populations on Caribbean reefs could negatively impact some of the most common scleractinian species remaining.

These mixed competitive outcomes suggest that environmental context could be important for mediating winners and losers among these species. Competition on reefs can be mediated by biotic and abiotic drivers such as predation (Hill 1998; Loh et al., 2015), spatial arrangement (Idjadi and Karlson 2007), light (Benayahu and Loya 1981), and size (Zilberberg and Edmunds 2001). Thus, the outcomes of some competitive interactions are often context dependent and changing environmental conditions may create situations where typically inferior competitors can outcompete superior competitors. For example, at Palmyra Atoll iron enrichment from a grounded ship has been implicated in promoting growth of *Rhodactis howesii* and inducing a shift from a coral-dominated reef to one completely overgrown by this corallimorph (Work et al., 2008). Nutrient pollution is a pervasive stressor

on coral reefs across the globe (Halpern et al., 2008; Ban et al., 2014), particularly on Florida reefs which are situated next to a population of ~6 million people (Ward-Paige et al., 2005). Thus, an overlooked but important effect of nutrient pollution on reefs could be the alteration of competitive outcomes, potentially contributing to observed shifts in benthic community assemblages (Smith et al. 2001; Burman et al., 2012; Darling et al., 2012; Perry et al., 2015; Cruz et al., 2016). While we could not find any experiments testing the effects of nutrient enrichment on competitive outcomes among benthic invertebrates, this research direction seems worthwhile as nutrient availability often dictates competitive outcomes in other communities (Fourqurean et al., 1994; Burson et al., 2018).

Alternatively, shifts in top-down control may now favor species that are competitively superior but have historically been kept at low abundance by predators. For example, overfishing of Caribbean reefs has relaxed top-down pressure by removing spongivorous fishes, potentially resulting in an increased abundance of sponges and more frequent overgrowth of scleractinians (Loh et al., 2015; Loh and Pawlik, 2014). Alternatively, predation could increase on scleractinians as coral populations decline (Burkepile 2012). Either or both scenarios could alter competitive outcomes to favor non-scleractinians in competitive interactions to reshape benthic communities.

Sponges in particular are increasing in abundance on many Caribbean coral reefs and may be benefiting from anthropogenically-modified conditions (Maliao et al., 2008; McMurray et al., 2010; Pawlik, 2011; Pawlik et al., 2016). *Aplysina fistularis* was not only the most abundant focal species but was also overgrowing competitors in most interactions, suggesting that *Ap. fistularis* thrives under the current conditions on Florida reefs. While our other focal species did not grow when competing, *Ap. fistularis* increased in size 31.8

$\pm 3.24\%$ and in most instances, overgrew the live tissue of its' competitors. These observations corroborate recent coral-sponge interaction work (Loh et al., 2015), and suggest overgrowth as a potentially important mechanism driving recent increased sponge abundance on reefs in Florida and the Caribbean (McMurray et al., 2010; Ruzicka et al., 2013). While our experiment only included one sponge species, sponges are frequently competitively dominant when released from predation (Wulff, 2006; Loh et al., 2015). Future studies that include multiple sponge species will further our ability to generalize how dominant sponges are as competitors and how changing conditions on Caribbean coral reefs influences their competitive abilities.

The changing environment on reefs may not only alter competitive abilities but could also dictate the utility of particular life history strategies. Both the Universal Adaptive Strategy theory (Grime 1977) and the Intermediate Disturbance Hypothesis (Connell 1978) suggest that highly competitive species should decline as disturbances and stress increase. We found that three of the four non-scleractinian species we studied were able to defend space on the reef by reducing the live area of their competitors (Figure 4a). The only scleractinian that reduced competitors' live area, *O. faveolata*, is now extremely rare on Florida reefs (Ruzicka et al. 2013). However, most aggressive species were unable to translate the death of competitors' tissue into growth gains and only one aggressive species (*Ap. fistularis*) increased in size. Indeed, organisms which devote significant resources to compete with neighbors often have less energy to devote to growth (Huot et al. 2014).

In contrast, *P. porites* and *S. siderea* were the least aggressive species, yet accounted for ~96% of the non-restored corals (i.e. *Ac. cervicornis*) in our surveys and are now two of the most common corals on Florida reefs (Burman et al., 2012). Darling et al. (2012) classify *P.*

porites and *S. siderea* as ruderal and stress-tolerant species, respectively, life history strategies predicted to thrive under high-disturbance or sub-optimal conditions. In our study, even though *P. porites* consistently lost aggressive interactions with competitors, they did not experience a decline in live tissue area (Figure 4b). This was likely due to the fact that on our experimental pucks, *P. porites* could grow away from competitors to escape competition, which occurred in ~39% of experimental *P. porites* colonies (Table 1). However, the substantial reduction in growth relative to controls suggests competition exacted a heavy physiological cost. Thus, current conditions on Caribbean reefs may favor species with more tolerant strategies that allocate less energy towards competition and more towards withstanding environmental stressors and growing into unoccupied space. However, as unoccupied space becomes more limiting, the consequences of competition are likely to become more severe for weaker competitors.

As global change reconfigures communities (Gilman et al., 2010; Urban et al., 2012), understanding how sessile invertebrates interact on the reefs of the future will be critical to management and restoration efforts. For example, 100% of the *Ac. cervicornis* competing with *E. caribaeorum* died. In contrast, *Ac. cervicornis* overgrew *Ap. fistularis* 100% of the time in field surveys (n=5) and grew by ~60% when placed next to *P. porites*. Such information could be used to inform coral restoration efforts, which primarily focus on outplanting nursery raised *Ac. cervicornis* colonies onto degraded reefs (Ladd et al., 2018). Specifically, when selecting reefs and sites within a reef to outplant corals, our findings suggest that restoration practitioners could avoid or remove species like *E. caribaeorum*, which are particularly harmful to *Ac. cervicornis*. Likewise, the high growth of *Ac.*

cervicornis when competing with *P. porites* suggests that *P. porites* may be a good candidate for mixed species outplanting to increase the diversity of corals being restored.

The assemblages of benthic communities on Caribbean coral reefs are changing as scleractinians decline and other benthic invertebrates become more common (Burman et al., 2012; Ruzicka et al., 2013; Perry et al., 2015). Competition has traditionally played a strong role in structuring benthic communities, yet the uncertain future of coral reefs requires a better understanding of the processes that will shape the reefs of the future. Our study suggests that competition among sessile invertebrates is likely to remain an important process in structuring coral reefs, but the optimal strategies for maintaining space on the benthos may change. We show that there is a competitive network among some of the common space holders on contemporary Caribbean reefs. While some scleractinians were strong competitors in both natural and experimental settings, these corals were either extremely rare (*O. faveolata*) or only present where coral restoration had been conducted (*Ac. cervicornis*). Instead, the most common corals were those that could either tolerate competition or grow into open substrate. In contrast, new dominants on Caribbean reefs, such as *E. caribaeorum*, *Ap. fistularis*, and *P. caribaeorum*, outcompeted other benthic invertebrates, including the most common scleractinians. Thus, the growing frequency of disturbances such as bleaching events and disease outbreaks on contemporary Caribbean reefs may shift communities from aggressive, highly competitive corals to favor species with ruderal or stress tolerant strategies (Darling et al., 2012). Manipulative experiments can contribute to our understanding of the mechanistic underpinnings of benthic spatial competition and help to predict competitive outcomes on reefs of the future. Ultimately, such results could be used to generate a

theoretical framework that predicts future changes in coral reef community structure and how anthropogenic forcing may drive these changes.

E. Acknowledgements

This work was conducted under permits FKNMS-2011-159, FKNMS-2014-060, FKNMS-2014-073, SAL-14-1579, and facilitated by a grant from the National Science Foundation, Biological Oceanography program (OCE-1130786) to DEB. We thank the Florida Keys National Marine Sanctuary coral nursery in Key West and the Coral Restoration Foundation for providing corals for this experiment. We thank A. Durán, S. Csik, L. Shaver, C. Fuchs, M. Roycroft, and S. Ladd for assistance in the field.z

F. References

- Alvarez-Filip L, Cote IM, Gill JA, Watkinson AR, Dulvy NK (2011) Region-wide temporal and spatial variation in Caribbean reef architecture: Is coral cover the whole story? *Glob Chang Biol* 17:2470–2477
- Álvarez-Noriega M, Baird AH, Dornelas M, Madin JS, Connolly SR (2018) Negligible effect of competition on coral colony growth. *Ecology* 99:1347–1356
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25–38
- Aronson R, Macintyre I, Wapnick C, O'Neill M (2004) Phase shifts, alternative states, and the unprecedented convergence of two reef systems. *Ecology* 85:1876–1891
- Baird A, Hughes T (2000) Competitive dominance by tabular corals: an experimental analysis of recruitment and survival of understorey assemblages. *J Exp Mar Bio Ecol* 251:117–132

- Ban SS, Graham NAJ, Connolly SR (2014) Evidence for multiple stressor interactions and effects on coral reefs. *Glob Chang Biol* 20:681–697
- Barabás G, J. Michalska-Smith M, Allesina S (2016) The effect of intra- and interspecific competition on coexistence in multispecies communities. *Am Nat* 188:E1–E12
- Bastidas C, Bone D (1996) Competitive strategies between *Palythoa caribaeorum* and *Zoanthus sociatus* (Cnidaria: Anthozoa) at a reef flat environment in Venezuela. *Bull Mar Sci* 59:543–555
- Bates D, Machler M, Bolker B, Walker S (2015) Fitting linear mixed-effects models using lme4. *J Stat Softw* 67:1-48
- Benayahu Y, Loya Y (1981) Competition for space among coral-reef sessile organisms at Eilat, Red Sea. *Bull Mar Sci* 31:514–522
- Birrell CL, McCook LJ, Willis BL (2005) Effect of algal turfs and sediment on coral settlement. *Mar Pollut Bull* 51:408-414
- Burkepile DE (2012) Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. *Coral Reefs* 31:111–120
- Burman S, Aronson R, van Woesik R (2012) Biotic homogenization of coral assemblages along the Florida reef tract. *Mar Ecol Prog Ser* 467:89–96
- Burson A, Stomp M, Greenwell E, Grosee J, Huisman J (2018) Competition for nutrients and light: testing advances in resource competition with a natural phytoplankton community. *Ecology* 99:1108–1118
- Buss LW, Jackson JBC (1979) Competitive networks: nontransitive competitive relationships in cryptic coral reef environments. *Am Nat* 113:223–234
- Chadwick NE, Morrow KM (2011) Competition among sessile organisms on coral reefs. In:

- Dubinsky Z., Stambler N. (eds) Coral Reefs: An Ecosystem in Transition. Springer Netherlands, Dordrecht, pp 347–371
- Chornesky E (1989) Repeated reversals during spatial competition between corals. *Ecology* 70:843–855
- Connell J (1961) The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus Stellatus*. *Ecology* 42:710–723
- Connell JH (1978) Diversity in tropical rain forests and coral reefs. *Science* 199:1302–1310
- Connell JH, Huges TP, Wallace CC, Tanner JE, Harms KE, Kerr AM (2004) A long-term study of competition and diversity of corals. *Ecol Monogr* 74:179–210
- Cruz ICS, Meira VH, de Kikuchi RKP, Creed JC (2016) The role of competition in the phase shift to dominance of the zoanthid *Palythoa* cf. *variabilis* on coral reefs. *Mar Environ Res* 115:28–35
- Darling ES, Alvarez-Filip L, Oliver TA, McClanahan TR, Côte IM (2012) Evaluating life-history strategies of reef corals from species traits. *Ecol Lett* 15:1378–1386
- Descombes P, Wisz MS, Leprieur F, Parravicini V, Heine C, Olsen SM, Swingedouw D, Kulbicki M, Mouillot D, Pellissier L (2015) Forecasted coral reef decline in marine biodiversity hotspots under climate change. *Glob Chang Biol* 21:2479–2487
- Diamond JM (1978) Niche shifts and the rediscovery of interspecific competition. *Am Sci* 66:322–331
- Fourqurean JW, Powell GVN, Kenworthy JW, Zieman JC (1994) The effects of long-term manipulation of nutrient supply on competition between the seagrasses *Thalassia testudinum* and *Halodule wrightii* in Florida Bay. *Oikos* 72:349–358
- Gardner T, Côté I, Gill J, Grant A, Watkinson A (2003) Long-term region-wide declines in

Caribbean corals. *Science* 301:958–960

Gilman SE, Urban MC, Tewksbury J, Gilchrist GW, Holt RD (2010) A framework for community interactions under climate change. *Trends Ecol Evol* 25:325–331

Gladfelter E (1978) Growth rates of five reef-building corals in the northeastern Caribbean. *Bull Mar Sci* 28:728–734

González-Rivero M, Yakob L, Mumby PJ (2011) The role of sponge competition on coral reef alternative steady states. *Ecol Modell* 222:1847–1853

González-Rivero M, Bozec YM, Chollett I, Ferrari R, Schönberg CHL, Mumby PJ (2016) Asymmetric competition prevents the outbreak of an opportunistic species after coral reef degradation. *Oecologia* 181:161–173

Graham NAJ, Jennings S, MacNeil MA, Mouillot D, Wilson SK (2015) Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* 518:94–97

Grime J (1977) Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *Am Nat* 111:1169–1194

Grottoli AG, Warner ME, Levas SJ, Aschaffenburg MD, Schoepf V, McGinley M, Baumann J, Matsui Y (2014) The cumulative impact of annual coral bleaching can turn some coral species winners into losers. *Glob Chang Biol* 20:3823–3833

Halpern BS, Walbridge S, Selkoe KA, Kappel C V., Micheli F, D'Agrosa C, Bruno JF, Casey KS, Ebert C, Fox HE, Fujita R, Heinemann D, Lenihan HS, Madin EMP, Perry MT, Selig ER, Spalding M, Steneck R, Watson R (2008) A global map of human impact on marine ecosystems. *Science* 319:948–952

Hill MS (1998) Spongivory on Caribbean reefs releases corals from competition with sponges. *Oecologia* 117:143–150

- Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, Harvell CD, Sale PF, Edwards AJ, Caldeira K, Knowlton N, Eakin CM, Iglesias-Prieto R, Muthiga N, Bradbury RH, Dubi A, Hatziolos ME (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742
- Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, Baird AH, Baum JK, Berumen ML, Bridge TC, Claar DC, Eakin CM, Gilmour JP, Graham NAJ, Harrison H, Hobbs JPA, Hoey AS, Hoogenboom M, Lowe RJ, McCulloch MT, Pandolfi JM, Pratchett M, Schoepf V, Torda G, Wilson SK (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83
- Huot B, Yao J, Montgomery BL, He SY (2014) Growth-defense tradeoffs in plants: A balancing act to optimize fitness. *Mol Plant* 7:1267–1287
- Idjadi JA, Karlson RH (2007) Spatial arrangement of competitors influences coexistence of reef-building corals. *Ecology* 88:2449–2454
- Jackson JBC, Buss L (1975) Alleopathy and spatial competition among coral reef invertebrates. *Proc Natl Acad Sci* 72:5160–5163
- Jackson JBC, Donovan MK, Cramer KL, Lam W (2014) Status and Trends of Caribbean Coral Reefs : 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland
- Karlson R (1980) Alternative competitive strategies in a periodically disturbed habitat. *Bull Mar Sci* 30:894–900
- Kemp DW, Oakley CA, Thornhill DJ, Newcomb LA, Schmidt GW, Fitt WK (2011) Catastrophic mortality on inshore coral reefs of the Florida Keys due to severe low-temperature stress. *Glob Chang Biol* 17:3468–3477

- Knowlton N (2001) The future of coral reefs. *Proc Natl Acad Sci U S A* 98:5419–25
- Ladd MC, Miller MW, Hunt JH, Sharp WC, Burkepile DE (2018) Harnessing ecological processes to facilitate coral restoration. *Front Ecol Environ* 16:239-247
- Lang J (1973) Interspecific aggression by scleractinian corals. 2. Why the race is not only to the swift *Bull Mar Sci* 23:260–279
- Lang JC, Chornesky E (1990) Competition between Scleractinian reef corals - a review of mechanisms and effects. In: Dubinsky Z. (eds) *Coral Reefs*. Elsevier Science Publishers, Amsterdam, pp 209–252
- Loh T-L, McMurray SE, Henkel TP, Vicente J, Pawlik JR (2015) Indirect effects of overfishing on Caribbean reefs: sponges overgrow reef-building corals. *PeerJ* 3:e901
- Loh T-L, Pawlik JR (2014) Chemical defenses and resource trade-offs structure sponge communities on Caribbean coral reefs. *Proc Natl Acad Sci* 111:4151–4156
- Maliao RJ, Turingan RG, Lin J (2008) Phase-shift in coral reef communities in the Florida Keys National Marine Sanctuary (FKNMS), USA. *Mar Biol* 154:841–853
- Marcus J, Thorhaug A (1981) Pacific versus Atlantic responses of the subtropical hermatypic coral *Porites* spp. to temperature and salinity effects. *Proceedings of the 4th International Coral Reef Symposium* 2:15–20
- McMurray SE, Henkel TP, Pawlik JR (2010) Demographics of increasing populations of the giant barrel sponge *Xestospongia muta* in the Florida Keys. *Ecology* 91:560–570
- McMurray SE, Finelli CM, Pawlik JR (2015) Population dynamics of giant barrel sponges on Florida coral reefs. *J Exp Mar Bio Ecol* 473:73–80
- Pawlik JR (2011) The chemical ecology of sponges on Caribbean reefs: Natural products shape natural systems. *Bioscience* 61:888–898

- Pawlik JR, Burkepile DE, Thurber RV (2016) A vicious circle? Altered carbon and nutrient cycling may explain the low resilience of Caribbean coral reefs. *Bioscience* 66:470–476
- Perry CT, Steneck RS, Murphy GN, Kench PS, Edinger EN, Smithers SG, Mumby PJ (2015) Regional-scale dominance of non-framework building corals on Caribbean reefs affects carbonate production and future reef growth. *Glob Chang Biol* 21:1153-1164
- Powell A (2010) Patterns of sponge abundance across a gradient of habitat quality in the Wakatobi Marine National Park, Indonesia. *Open Mar Biol J* 4:31–38
- Precoda K, Allen AP, Grant L, Madin JS (2017) Using traits to assess nontransitivity of interactions among coral species. *Am Nat* 190:420-429
- R Core Team (2017) R: A Language and Environment for Statistical Computing
- Ruzicka R, Colella M, Porter J, Morrison J, Kidney J, Brinkhuis V, Lunz K, Macaulay K, Bartlett L, Meyers M, Colee J (2013) Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Mar Ecol Prog Ser* 489:125–141
- Sebens KP, Miles JS (1988) Sweeper tentacles in a gorgonian octocoral: morphological modifications for interference competition. *Biol Bull* 175:378
- Smith JE, Smith CM, Hunter CL (2001) An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs* 19:332–342
- Swierts T, Vermeij MJA (2016) Competitive interactions between corals and turf algae depend on coral colony form. *PeerJ* 4:e1984
- Urban MC, Tewksbury JJ, Sheldon KS (2012) On a collision course: competition and dispersal differences create no-analogue communities and cause extinctions during

- climate change. Proc R Soc B Biol Sci 279:2072–2080
- Wahle CM (1980) Detection, pursuit, and overgrowth of tropical gorgonians by milleporid hydrocorals: perseus and medusa revisited. Science 209:689–91
- Walker RP, Thompson JE, Faulkner DJ (1985) Exudation of biologically-active metabolites in the sponge *Aplysina fistularis* - II. Chemical evidence. Mar Biol 88:27–32
- Ward-Paige CA, Risk MJ, Sherwood OA, Jaap WC (2005) Clionid sponge surveys on the Florida Reef Tract suggest land-based nutrient inputs. Mar Pollut Bull 51:570–9
- Wegener C, Martin B, Didden C, Edmunds PJ (2018) Overgrowth of Caribbean octocorals by milleporid hydrocorals. Invertebr Biol 137:29–37
- Wellington GM (1980) Reversal of digestive interactions between Pacific reef corals: mediation by sweeper tentacles. Oecologia 47:340–343
- van Woesik R, Scott WJ, Aronson RB (2014) Lost opportunities: coral recruitment does not translate to reef recovery in the Florida Keys. Mar Pollut Bull 88:110–117
- Work TM, Aeby GS, Maragos JE (2008) Phase shift from a coral to a corallimorph-dominated reef associated with a shipwreck on Palmyra atoll. PLoS One 3:1–5
- Wulff JL (2006) Ecological interactions of marine sponges. Can J Zool 84:146–166
- Zilberberg C, Edmunds PJ (2001) Competition among small colonies of *Agaricia*: The importance of size asymmetry in determining competitive outcome. Mar Ecol Prog Ser 221:125–133

IV. Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes

With Deron E. Burkepile and Andrew A. Shantz

Reprinted by permission from John Wiley and Sons: Ladd, M.C., Burkepile D.E., and Shantz, A.A. 2019. Near-term impacts of coral restoration on target species, coral reef community structure, and ecological processes. *Restoration Ecology*.

A. Introduction

Coral reefs, along with the ecological and ecosystem services they provide, are being lost at an alarming rate (Hoegh-Guldberg et al. 2007; Hughes et al. 2017). Although coral reefs only cover <0.1% of Earth's surface, they rival the species diversity of rainforests, housing more than 30% of marine biodiversity (Reaka-Kudla 2005) and provide innumerable ecosystem services including protein (Burke & Maidens 2004; de Groot et al. 2012) and shoreline protection for >100 million people living near coastlines (Ferrario et al. 2014). However, in the past half-century, nearly half of the corals on Pacific reefs have been lost (Bruno & Selig 2007; Hughes et al. 2017). Similarly, Caribbean reefs have been decimated by an approximately 80% decline in coral cover (Jackson et al. 2014). This drastic loss of coral stems from a combination of stressors such as overfishing, coastal development, pollution, and rising ocean temperatures (Zaneveld et al. 2016; Hughes et al. 2018), with degraded reefs often experiencing positive feedbacks that maintain them in a degraded state (Mumby 2009). Thus, there is an urgent need for strategies to effectively facilitate the recovery of degraded reefs while also preventing further coral loss.

Coral restoration, i.e. actively enhancing coral populations, is an increasingly popular approach to confront local declines in coral abundance (Bayraktarov et al. 2016; Ladd et al. 2018). Inspired by successful restoration strategies used to restore other habitats, contemporary coral restoration approaches primarily consist of outplanting nursery-raised corals to degraded reefs (Young et al. 2012). Propagation and outplanting of nursery-grown corals has become so popular that over 150 restoration groups currently operate coral nurseries in more than 20 countries throughout Caribbean alone (Lirman & Schopmeyer 2016). As a result, coral restoration efforts are increasingly capable of augmenting coral

populations at ecologically-meaningful scales (Miller et al. 2016; Montoya-Maya et al. 2016).

The primary goal of coral restoration has been to augment populations of target coral species. However, an implicit expectation is that restoring these foundation species will eventually drive reefs towards recovery by facilitating the development of coral and fish communities that can foster important functions like herbivory. While most coral restoration studies focus on the survival and growth of outplanted corals, few have investigated if and how restoration has impacted the reef community or important ecological processes (Ladd et al. 2018). This oversight poses a serious problem for restoration planning, as restoring singular components of an ecosystem may be necessary, but not sufficient, to drive the recovery of a community and restore important ecosystem functions (Palmer & Filoso 2009). If coral outplanting strategies do not generate positive feedbacks on community composition or ecosystem processes, restored reefs will be vulnerable to reoccurring decline and restoration practitioners should incorporate additional considerations to realize these benefits. Thus, quantitative studies detailing the effects of coral outplanting on community structure and ecosystem processes are sorely needed.

Here, we measured: (1) the effects of coral restoration on enhancing populations of the coral *Acropora cervicornis*, and (2) the potential cascading effects on community structure and ecosystem processes that may arise when coral populations are enhanced. To do so, we measured diversity, community structure, and ecological processes at four reefs in the Florida Keys, USA. On each reef we compared restored sites where corals were outplanted with unmanipulated control sites to assess the abundance, diversity, and community structure of corals and fishes present. Additionally, we investigated how restoration influenced proxies

for two important ecological processes: herbivory and corallivory. We hypothesized that restored sites would have greater diversity and abundance of corals. In turn, we predicted that increased coral cover and diversity would lead to increased richness and biomass of fishes, enhancing herbivory rates and increasing the removal of invertebrate corallivores.

B. Methods

Study Sites

From July to August of 2014 we surveyed four reefs in the Florida Keys National Marine Sanctuary, USA (Appendix 10). Restoration using nursery-raised colonies of the threatened coral *Acropora cervicornis* began on a limited scale in the region in the early 2000's and has expanded rapidly since (Miller et al. 2016). We selected four reefs undergoing coral restoration: Molasses Reef (11 years of outplanting), Pickles Reef (6 years), Snapper Ledge (5 years), and Conch Reef (2 years). Although these sites differ in time since coral outplanting began, large scale restoration (i.e. 100's of corals yr⁻¹) did not begin until 2011 for all reefs (Appendix 11). Therefore, we chose these sites because they represent a gradient of outplanting effort spanning low (Snapper Ledge and Conch Reef; ~500 corals), moderate (Pickles Reef; ~1,150 corals), and high (Molasses Reef; ~2,300 corals) numbers of corals outplanted. Molasses and Pickles Reef are spur-and-groove reef formations, while Snapper Ledge and Conch Reef are ledge formations. Outplanted corals were secured to the substrate using a small amount of marine epoxy where branches contacted the benthos. At each reef, we conducted surveys within two sites along the main spur or ledge formations: restored sites where *A. cervicornis* colonies had been outplanted and non-restored control sites $\geq 5\text{m}$ away from the restored site along the same main ledge or an adjacent, parallel spur formation.

Control sites were located within the same reef, possessed similar topographical characteristics, and provide a characterization of benthic communities in the unrestored areas.

Community and Ecosystem Process Metrics

(1) *Diversity*: On reefs, coral diversity may be a particularly important indicator of ecosystem integrity as the physical structure provided by distinct corals creates important habitat (Syms & Jones 2000). Similarly, diverse assemblages of fishes are critical for structuring healthy reef communities: herbivores consume algae that compete with corals (Hughes et al. 2017; McCook et al. 2001), invertivores feed on coral predators (Ladd & Shantz 2016), and predators can shape the behavior of lower trophic groups (Catano et al. 2017).

We assessed differences in the abundance and diversity of corals and fishes in restored and control sites via transect surveys. Between 10h00 and 14h00, we swam ten 25x4m belt transects at each reef. Transect starting positions were chosen haphazardly but were laid out parallel to spur or ledge formations and remained completely within restored (i.e. *A. cervicornis* present) or control sites (n=5 in restored and control sites). A single diver swam the length of each transect and recorded the species and estimated sizes for all fishes >5cm total length before re-swimming the transect to identify and count cryptic and juvenile fishes <5cm. After completing the fish surveys, we counted every coral in a 25x2m swath along the same transect. For colonies ≥ 5 cm in diameter, we identified the coral to the species level, and measured each coral along its longest diameter and at the widest point perpendicular to the

first measurement. Additionally, we estimated the percent of each colony's surface without live tissue to assess partial mortality.

(2) *Community Structure*: Closely related to diversity, community structure represents the physiognomy and architecture of the biological community (SER, 2004). Changes in coral communities and accompanying structural complexity influence the biomass and richness of other invertebrate and fish species (Komyakova et al. 2013). Further, alterations to fish community structure can impact functional redundancy and complementarity among community members, which are often vital for maintaining reef resilience (Burkepile & Hay 2008).

For coral communities, we multiplied colony size measures to estimate the surface area of each colony and summed the total area of all colonies to calculate the percent cover of coral on each transect. Additionally, we calculated the total linear extension (TLE) m^2 for *A. cervicornis* using conversions from Kiel et al. (2012). Total linear extension is a common measurement of *A. cervicornis* that more accurately captures the 3-dimensional habitat than colony area (Huntington et al. 2017). To assess the effect of coral restoration on site-wide structural complexity, we measured rugosity every 5m along our transects by measuring the difference between the lowest and highest point on the reef within a 1m radius (Ladd & Collado-Vides 2013). These measurements were averaged to generate an estimate of rugosity for each transect. For fish communities, we used published length-weight relationships (Bohnsack & Harper 1988; Marks & Klomp 2003) to estimate the biomass of each species and functional group (e.g., piscivores, invertivores, herbivores) observed within each transect.

To examine if restoration influenced younger cohorts of coral and fish populations, we compared the abundance of juvenile corals (surface area $<16\text{cm}^2$ *sensu* Ritson-Williams et al. (2009)) and fishes (juvenile life stage or $<5\text{cm}$; excluding small-bodied damselfishes, gobies, and blennies) in restored versus control sites. However, since only corals $\geq 5\text{cm}$ length in one diameter were recorded, we stress that our results provide conservative estimates of the abundance of juvenile-sized corals.

(3) *Ecological Processes*: Promoting ecological processes and interactions between community members is a fundamental goal of ecological restoration (SER, 2004). We assessed the impact of coral restoration on proxies for two important processes: herbivory and corallivory. Herbivory is one of the strongest drivers of benthic community composition on reefs (Burkepile & Hay 2006). Sufficient herbivory can prevent reefs from becoming dominated by algae and is critical for maintaining coral-dominated habitats (Adam et al. 2011). In contrast, corallivory can significantly damage corals (Rotjan & Lewis 2008), remove tissue at rates that far outpace coral growth (Baums et al. 2003), spread coral diseases (Williams & Miller 2005), and make corals more susceptible to thermal stress (Shaver et al. 2018).

To assess how restoration affected herbivory, we measured grazing intensity in restored and control sites using assays of *Thalassia testudinum*, a ubiquitous, palatable seagrass commonly used to quantify grazing pressure on reefs (e.g. Catano et al. 2017; Lewis 1986). Each morning we gathered *T. testudinum* from a nearby seagrass bed. Each blade was cut to 10cm length, cleaned of epiphytes, and secured to a clothespin. We secured clusters of 5 clothespins together and deployed assays at 5m and 20m along each transect after completing our fish and coral surveys. We left the assays undisturbed for one hour before collecting and

re-measuring the remaining seagrass length to quantify consumption. To assess how restoration influenced corallivore abundance, we counted the two most common invertebrate corallivores in the Florida Keys, *Coralliophila abbreviata* and *Hermodice carunculata*, on each coral surveyed and recorded whether signs of disease were present. However, *H. carunculata* were so rare that we did not explore these data quantitatively.

Statistical Analysis

We tested for differences in coral cover, fish biomass, juvenile coral and fish abundance, and rugosity using separate mixed-effects ANOVAs with treatment (restored or control) as a fixed factor and reef as an interacting random effect. We used similar models to test whether the biomass or density of fish functional groups responded to restoration by including functional group as an interacting fixed factor. Coral cover and juvenile coral abundance were logit transformed and fish biomass and abundance log transformed to meet assumptions of ANOVA. Additionally, we tested whether restoration impacted the abundance of common and ecologically important fish genera and species by subtracting the number of individuals found in a restored site from the number found in the paired control site. For each group, we used t-tests to determine if the difference in fish abundance differed from zero, with values significantly greater than zero indicating an increase in abundance with restoration and values less than zero indicating declining species abundance.

We used a combination of PERMANOVA and SIMPER analyses based on Bray-Curtis distances to examine differences in the species composition of corals and fishes at restored and control areas. PERMANOVA models used 9,999 permutations and considered site (4 levels) and treatment (2 levels) as interacting fixed factors with transect nested within site.

To examine species diversity, we calculated the Shannon-Wiener index (H) for corals and fishes based on species abundance. Because species diversity and richness were highly variable between transects, we pooled the observations within control and restored sites at each reef and tested for differences in H and species richness between restoration regimes using a paired t-test.

We tested for differences in the percent of seagrass assays consumed using a mixed-effects ANOVA with treatment as a fixed factor and site a random, interacting effect. To avoid violating assumptions of independence, we nested each assay within the transect on which it was deployed. Percent seagrass consumed was logit transformed to normalize the distribution of the residuals. Corallivorous snail abundance, coral mortality, and disease prevalence data were heavily skewed towards zero. Therefore, we used Pearson's Chi-squared tests to determine whether restoration impacted the probability that snails were present on corals or that corals were experiencing tissue mortality. We used Fisher's test to explore whether snail presence influenced the probability that a coral displayed signs of disease. For this analysis, we only compared corals within restored areas because there were no observations of corals with both snails and disease in control sites.

The effects of restoration may depend on the density of restored corals, which could influence important processes like disease dynamics and the aggregation of fishes (Ladd et al. 2016; Huntington et al. 2017). We used linear mixed effects models to test how the mean density (cm TLE m⁻²) and the percent cover of restored *A. cervicornis* along each transect impacted six responses in the restored reef community: density of *C. abbreviata*, percent of seagrass assays consumed, the density of all fish, fishes <15cm TL, juvenile fish, and damselfish, which are most likely to utilize the habitat created by *A. cervicornis*

(Schopmeyer & Lirman 2015), as well as two metrics of coral health: partial mortality and the frequency of diseased coral colonies. For all of these models, reef was included as a random effect.

All analyses were conducted using R Version 3.3.2 (R Core Team 2016). PERMANOVA analyses were conducted using the *vegan* package (Oksanen et al. 2018). Mixed-effects ANOVAs were carried out using the *nlme* package (Pinheiro et al. 2015). P-values from these models were calculated via Wald F-tests using Satterthwaite approximate degrees of freedom in the *car* package (Fox et al. 2012). When we detected significant interactions in the main models, we tested for differences between treatments within reefs via post hoc analyses corrected for false discovery rates using the *multcomp* package (Hothorn et al. 2008).

C. Results

Restoration Effects on Coral Communities

Across all four reefs, we observed 23 coral species within restored sites and 19 species at control sites (Appendix 12). Coral communities did not differ in diversity between restored ($H=1.52 \pm 0.10$; mean \pm SE) and control sites (1.61 ± 0.12 ; $P=0.33$). However, coral cover differed among reefs ($\chi^2(3)=9.14$, $P=0.027$; Figure 1) and was consistently higher in restored sections of the reef than in adjacent control sites ($\chi^2(1)=215.68$, $P<0.001$).

Within-site differences in coral cover were driven by the presence of outplanted *Acropora cervicornis* colonies, which comprised >75% of coral cover in restored sites. Surprisingly, although coral cover was nearly 4x higher in restored- vs control areas, we detected no difference in rugosity within ($\chi^2(1)=0.76$, $P=0.382$) or among reefs ($\chi^2(3)=1.02$,

P=0.797). There was a significant Treatment x Reef effect on the abundance of non-acroporid juvenile-sized corals ($\chi^2(3)=12.00$, P=0.007; Figure 2), with juvenile-sized corals more abundant in the restored site at Pickles Reef than the control site, but no differences at the other reefs. The high abundance of *A. cervicornis* in restored areas drove differences in coral communities (PERMANOVA: $F_{1,32}=22.17$, P<0.001), with 48% of the dissimilarity attributable to *A. cervicornis* (Appendix 13). When we excluded *A. cervicornis* from our analysis, the differences between control and restored coral communities were no longer present (PERMANOVA: $F_{1,32}=0.96$, P=0.47).

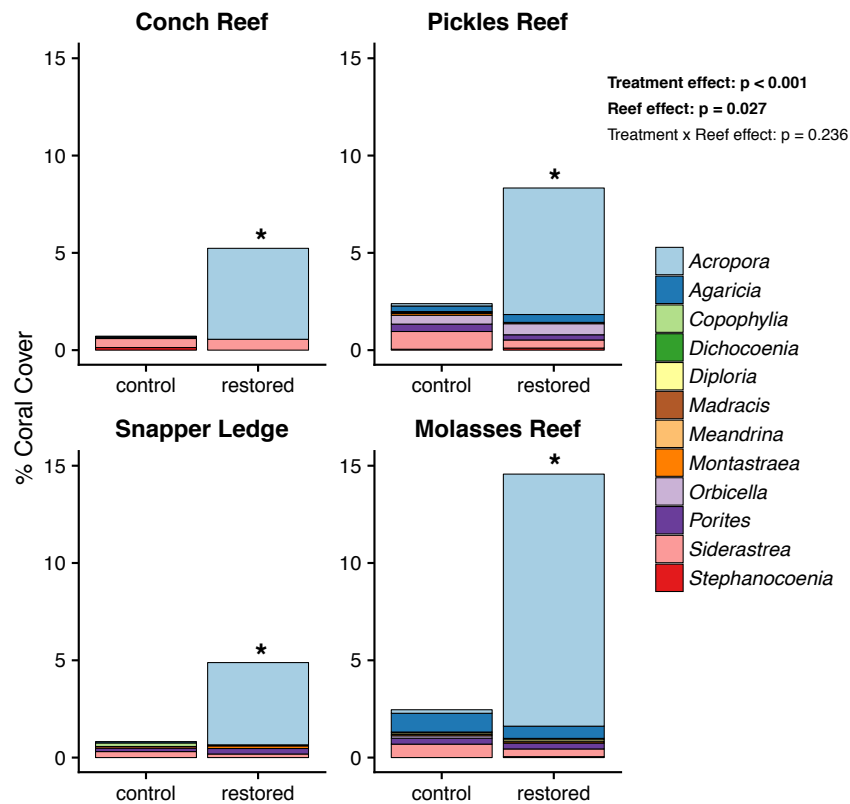


Figure 1. Mean percent cover of corals by genera in restored vs. control sites at the four reefs surveyed. Data presented are pooled from all transects within a reef and restoration treatment (n = 5 for both restored and control sites). Statistics from mixed effects ANOVA. Asterisks indicate significant differences (p < 0.05) in coral cover between restored and control sites within a reef from post hoc tests with Tukey's correction.

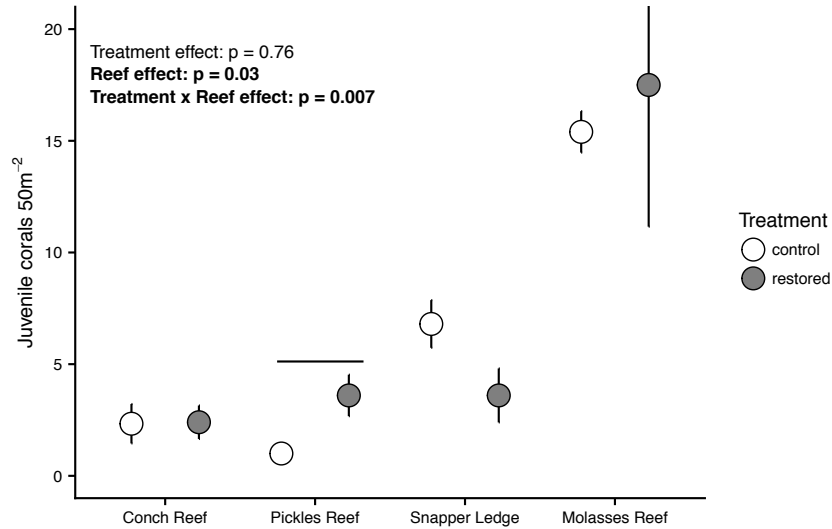


Figure 2. Abundance (individuals 50 m⁻²) of juvenile-sized corals (surface area < 16 cm²) observed in restored vs. control sites at each reef. Statistics from mixed effects ANOVA. A line over points indicates significant within-reef differences ($p < 0.05$) in the abundance of juvenile-sized corals between restored and control sites from post hoc tests with Tukey's correction.

Restoration Effects on Fish Communities

Differences in coral cover between restoration regimes did not translate to changes in fish communities (PERMANOVA: Treatment Effect: $F_{1,32}=1.56$, $P=0.10$). Although we documented 66 fish species in control sites compared to 51 in restored sites, there was no difference in species richness (control: 41.25 ± 3.77 ; restored 36 ± 1.47 ; $p=0.22$) or diversity (control: $H=2.33 \pm 0.12$; restored: 2.22 ± 0.1 ; $P=0.33$). At Conch and Molasses Reef, average fish biomass was roughly 2.6x and 2.1x greater in control vs restored sites, respectively (Figure 3a). Conversely, at Pickles Reef fish biomass was 2x greater at the restored site, generating a significant Treatment x Reef interaction ($\chi^2(3)=10.94$, $P=0.012$). However, after correcting for multiple comparisons, we were unable to detect within-reef differences in total biomass between restored and control sites. Interestingly, damselfish (i.e. *Stegastes* spp. and *Microspathodon chrysurus*) occurred at 1.5x higher densities in restored sites than in control sites ($\chi^2(1)=11.72$, $P<0.001$; Figure 3b). There were no differences in the abundance of any

other fish taxa in restored versus control sites (Figure 3c). We also found no evidence that restoration influenced the density of juvenile fishes ($\chi^2(3)=0.12$, $P=0.730$; Figure 3d).

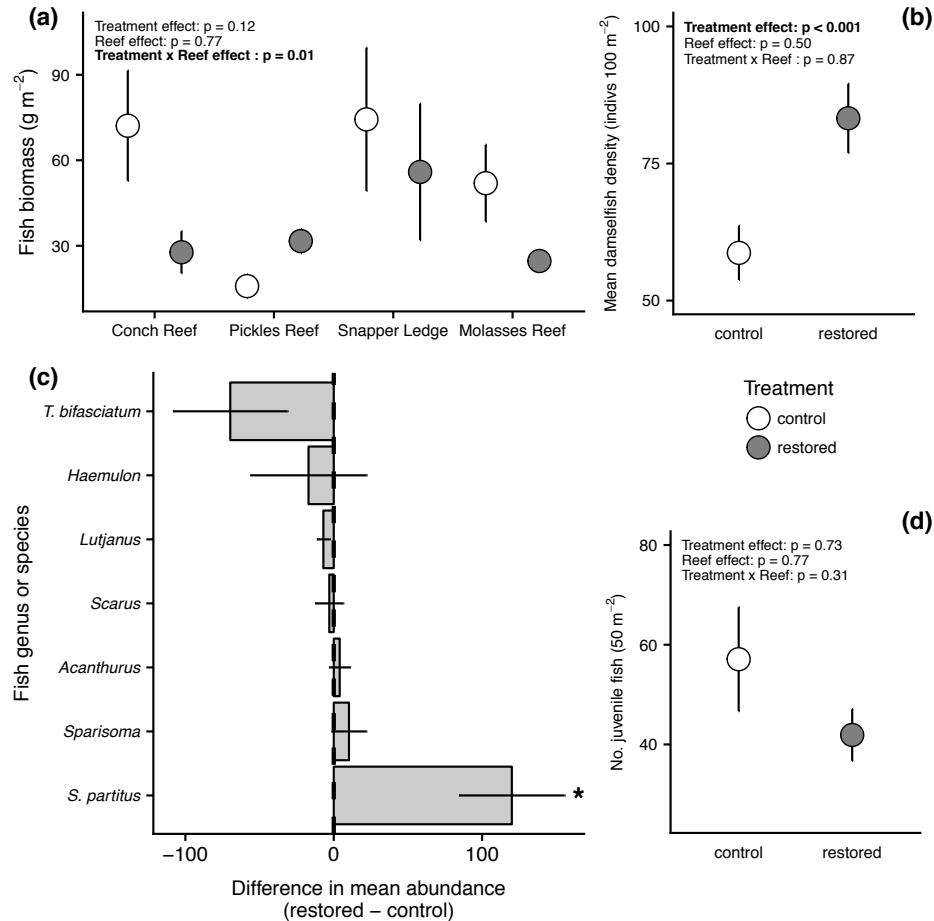


Figure 3. (a) Biomass of all fishes in restored vs. control areas at each reef and (b) mean damselfish density (individuals 100 m⁻²). (c) Difference in the mean abundance of fishes in restored vs. control areas for important genera and species of herbivores (*Acanthurus* spp., *Scarus* spp. and *Sparisoma* spp.), invertivores (*Haemulon* spp. and *Thalassoma bifasciatum*), piscivores (*Lutjanus* spp.), and the most common damselfish (*S. partitus*). Asterisk indicates difference in mean abundance significantly different from zero ($p < 0.05$). Statistics from t-test. (d) Abundance of juvenile fishes (< 5cm TL) in restored and control sites. Statistics from mixed effects ANOVA. Data are means \pm SE.

Restoration Effects on Ecological Processes

Although restoration had minimal effects on the biomass and density of fish, we found mixed evidence that herbivory and corallivory varied with restoration regimes. Herbivores were more abundant in the restored site at Pickles Reef (Treatment x Reef Effect:

$\chi^2(3)=10.51$, $P=0.015$; Appendix 14) and we found a significant Treatment x Reef effect on

the proportion of seagrass assays consumed ($\chi^2(3)=15.94$, $P=0.001$; Figure 4a). Surprisingly, grazing intensity was only significantly higher in restored sites at Conch Reef ($P=0.03$). Although not significant, restored sites also had $\sim 1.6x$ as many corallivorous snails as control sites ($\chi^2(1)=1.51$, $P=0.22$; Figure 4b). Similarly, we found $2x$ as many snails on *Orbicella* colonies in restored sites ($n=65$ on 6 coral colonies) than in control sites ($n=32$ on 9 coral colonies), though this difference was not statistically significant ($P=0.549$). Of the 306 *C. abbreviata* we recorded, 62% were found in restored sites, the majority of which were preying on *A. cervicornis*. Interestingly, within restored sites corals that were being actively preyed on by snails were $4.6x$ more likely to display signs of disease than corals without snails ($P<0.001$; Figure 4c).

Overall, disease prevalence was nearly $4x$ greater in restored sites than in control sites (11.63% vs. 2.92%, respectively), with *A. cervicornis* accounting for 86% of the documented instances of coral disease in restored habitats and 72.9% of all disease recorded. The remaining observations of disease-like symptoms were nearly exclusively from *Siderastrea siderea* colonies displaying signs of dark spot syndrome (DSS; 25.7% of all diseased coral observations). The percent of *S. siderea* colonies with DSS in control and restored sites was nearly identical (9.05 and 8.34%, respectively).

The proportion of colonies experiencing tissue mortality was also greater in restored sites than control sites ($\chi^2(1)=43.24$; $P<0.001$). Like disease prevalence, differences in the prevalence of partial mortality between restored and control sites were driven by *A. cervicornis*, 69% of which were experiencing some degree of tissue loss, compared to 39% of corals in control sites. When *A. cervicornis* were excluded from the analysis, the

difference in tissue mortality prevalence between restored and control sites was no longer present ($\chi^2(1)=0.706$; $P=0.40$).

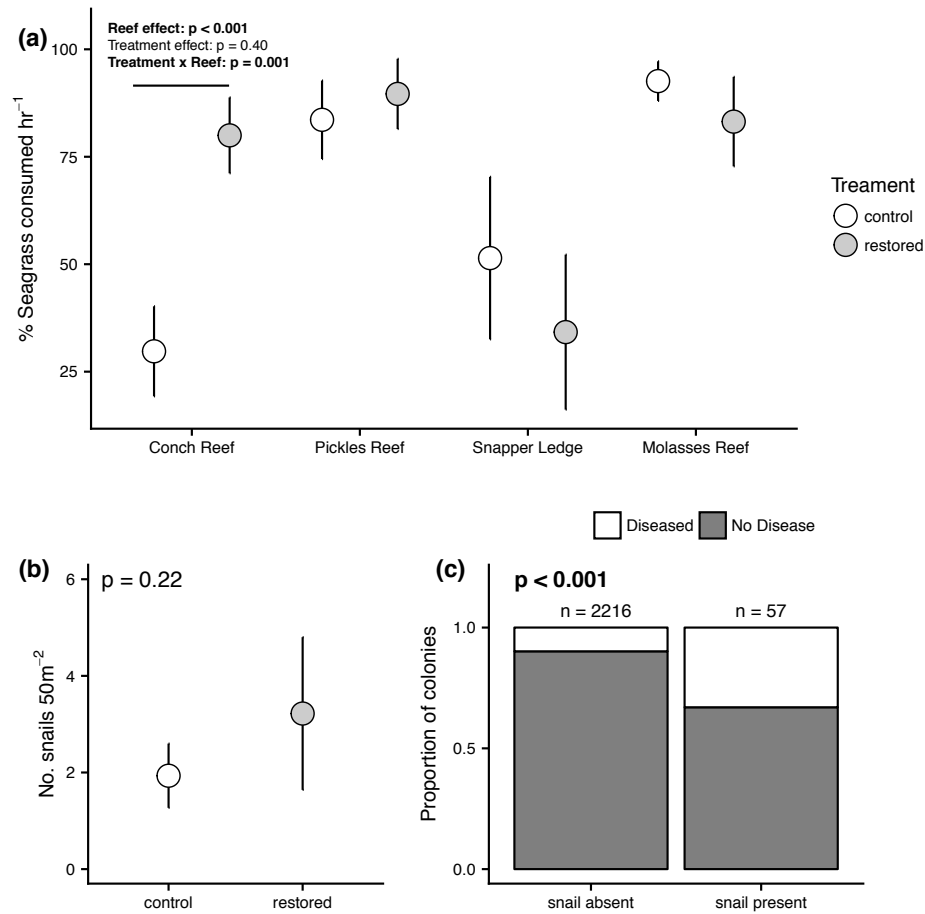


Figure 4. (a) Percent of seagrass assays consumed in restored vs. control sites at each reef. Statistics from mixed effects ANOVA. A line over points indicates significant within-reef differences ($p < 0.05$) in the consumption of seagrass assays between control and restored sites. (b) Abundance of the corallivorous snail *Coralliophila abbreviata* in restored vs. control sites. P-value from Pearson's Chi-squared test. Data are means \pm SE. (c) Proportion of coral colonies within restored areas with and without corallivorous snails present that were displaying signs of disease. Values above each bar represent the number of corals surveyed. P-value from Fisher's test comparing effect of snail presence on the probability that a coral displayed disease-like signs.

Effects of Outplant Density Within Restored Sites

Within restored sites, the density of *A. cervicornis* (TLE) ranged from 378 cm m⁻² at Molasses Reef to 113 cm m⁻² at Snapper Ledge. The percent cover of restored corals followed the same pattern and was on average highest at Molasses Reef (12.96%) and lowest at Snapper Ledge (3.98%). We found a marginal increase in mean partial colony mortality

with increased *A. cervicornis* density ($\chi^2(1)=3.305$; $P=0.07$), but no effect on disease prevalence ($\chi^2(1)=0.339$; $P=0.49$). Further, we found no relationship between *A. cervicornis* density ($\chi^2(1)=0.475$; $P=0.56$) or cover ($\chi^2(1)=0.567$; $P=0.45$) and the density of corallivorous snails, consumption of seagrass assays (density: $\chi^2(1)=1.859$; $P=0.17$; cover: ($\chi^2(1)=0.728$; $P=0.39$), or any of the four fish community metrics (Appendix 15).

D. Discussion

Here, we show that recent coral outplanting across multiple reefs in the Upper Florida Keys enhanced the local population of *A. cervicornis*, creating areas where this threatened species is now abundant. We found some evidence of increased herbivory, abundance of herbivorous fishes, and juvenile corals in areas where corals had been restored, but these effects were inconsistent across different reefs. Several taxa consistently responded positively to coral restoration. In particular, the density of damselfish was consistently higher in restored sites, and corals in restored areas had on average 1.6x more corallivorous snails compared to control sites. Corals in restored sites experienced a higher prevalence of disease and mortality, primarily driven by patterns of restored *A. cervicornis*. Thus, three years after large scale coral restoration began, the gains in coral density from restoration have persisted, but these gains have had inconsistent impacts on diversity, community structure, and ecological processes.

Numerous ecological processes and positive feedbacks posited to govern coral reef communities hinge on the physical structure provided by live corals (Mumby & Steneck 2008; Huntington et al. 2017). We expected that enhanced coral populations would foster changes in the physical structure of restored reefs and subsequently influence ecological

processes that shape coral reef communities. Yet, despite a ~4-fold increase in coral cover at restored sites, we found no measurable difference in topographic complexity between restored and control sites. This pattern was surprising given the three-dimensional complexity of outplanted *A. cervicornis* colonies. Several factors could potentially explain this unexpected result. First, the low rugosity found within restored sites may be partly due to restoration practitioners intentionally selecting relatively flat areas to facilitate outplanting. Alternatively, it is possible that the high degree of tissue mortality in outplanted corals limited the growth and structure created by *A. cervicornis*. Similarities in the size distribution of restored corals at these sites (Appendix 16) further suggests that the oldest outplants may have died, experienced partial mortality, or breakage, reducing the amount of structure created by restored corals. Finally, our method to quantify rugosity may have been too coarse to detect changes in rugosity generated by *A. cervicornis* outplants. However, if this absence of an effect was simply a result of the scale at which we measured rugosity, we would still expect responses in some component of the fish community, as recruit abundance of many reef fish is tightly linked to live coral cover (Holbrook et al. 2000; Graham 2014).

Overall, biomass and diversity of fishes did not differ with restoration across reefs. At the functional group level, herbivores were more abundant in the restored area at Pickles Reef but did not differ at any other reef. Roving herbivores like parrotfish and surgeonfish can have territories up to 1000 m² (Mumby and Wabnitz 2002; Catano et al. 2015). This area is large enough to span portions of both restored and control areas on the reefs we surveyed, which could make it difficult to detect differences in herbivore abundance between our treatments. In contrast, fishes such as grunts exhibit diurnal movement patterns, consistently sheltering at the same location on the reef for the entire day and leaving at night to forage in

nearby sand flats and seagrass beds (Ogden and Quinn 1989; Shantz et al. 2015). Thus, if coral restoration had augmented habitat enough to promote the aggregation of these fishes, we would have expected to see a response in this component of the fish community, even with the relatively small ($\geq 5\text{m}$) distance between our restored and control areas.

We observed taxa-specific responses to coral restoration, with higher densities of damselfishes in restored areas. Increased damselfish density was not entirely unexpected, as many Caribbean damselfishes are territorial, site-specific fishes that often colonize outplanted *A. cervicornis* (Schopmeyer & Lirman 2015). Life history may play a key role in determining what species are able to take advantage of increased habitat from restored corals and the rate at which they are able to colonize these new habitats. For example, *S. partitus*, which comprised the majority of damselfish observed, has fast generation times and high larval supply on reefs in the Florida Keys compared to longer lived species like parrotfishes and surgeonfishes (Grorud-Colvert & Sponaugle 2009), potentially allowing them to rapidly colonize coral outplants. Thus, the relatively short (3 years) time period between the start of large-scale coral outplanting and our study may not be sufficient time for longer-lived fishes to respond to enhanced structure on restored reefs. However, if *S. partitus* can quickly colonize restored corals, their territorial behavior, or simply physical occupation of limited habitat, can impact the ability of other fishes to recruit to these areas (Risk 1998; Almany 2004). Regardless of the mechanism, slow responses to increased habitat availability by functional groups that provide key ecological functions on reefs (e.g. herbivores) may be problematic for regaining ecosystem functions, particularly when large fishes play a disproportionate role in driving important ecological processes (Lokrantz et al. 2008).

We found limited evidence that coral restoration influenced herbivory as Conch Reef was the only reef that had higher herbivory rates in restored areas. The abundance of damselfish in restored areas may help explain this pattern. Although *S. partitus* are less aggressive and territorial than other damselfish species, they can influence patterns of herbivory within their territories (Williams et al. 2001) and were the most common fish in our surveys. Furthermore, while the average abundance of damselfish was 1.5x higher in restored sites compared to control sites, Conch Reef had the lowest damselfish density (mean=0.43 individuals m⁻² versus 0.68-1.11 at other sites). Interestingly, Conch Reef also had the shortest history of restoration effort, with just one year of coral outplanting when our surveys occurred, which may have limited the recruitment or establishment of damselfishes. Thus, the lower densities of damselfishes at Conch Reef may have allowed increased herbivory in restored areas. Territorial damselfishes can also modify the home ranges of numerous species of wrasses (Jones 2007), consistent with the inverse relationship we observed between *S. partitus* and *T. bifasciatum*. Accordingly, damselfishes rapidly colonizing outplanted *A. cervicornis* may delay or preclude the benefits of coral restoration to fish communities by inhibiting certain fish from using, aggregating, or recruiting to restored areas.

Similar to damselfishes, corallivorous snails (*C. abbreviata*) were 1.6x more abundant in restored sites than control sites, consistent with previous evidence for *C. abbreviata* preference for *A. cervicornis* (Johnston & Miller 2014). While this difference was not statistically significant, likely due to the high variability in this aggregating species, the ecological consequences could be important. *Coralliophila abbreviata* are known disease vectors (Williams & Miller 2005), and in our study disease was ~3x more prevalent on coral colonies with a snail present. Further, predation by *C. abbreviata* can make corals more

susceptible to thermal stress (Shaver et al. 2018). Thus, aggregating coral predators at restored sites could increase disease prevalence as well as reduce corals' ability to survive to thermal stress in these areas. However, excluding outplanted corals from our analysis revealed no differences in partial mortality or disease between restored and control areas, suggesting the negative impacts of increased corallivorous snail abundance were not transmitted to other corals. Thus, the higher prevalence of disease and partial mortality in restored sites is likely a consequence of *A. cervicornis*' high susceptibility to disease and partial mortality (Williams & Miller 2005; Miller et al. 2016).

High densities of corals may be necessary to initiate positive feedbacks that facilitate reef recovery. For example, positive relationships between *A. cervicornis* density and the abundance of schooling grunts may only be realized in areas with high coral densities (2,000-4,500 cm TLE m⁻²; Huntington et al. 2017). Schooling fishes can create nutrient hotspots that benefit nearby corals by enhancing growth and promoting algal removal by herbivores (Shantz et al. 2015). Alternatively, increased coral density at restored sites could intensify herbivory by reducing the available substrate for macroalgae, thereby concentrating existing herbivory on fewer available resources (Williams et al. 2001). Across the four reefs we surveyed, the average density of *A. cervicornis* ranged from 113-378 cm TLE m⁻², mirroring outplanting effort (i.e. number of colonies outplanted) at each reef. Accordingly, we found no relationship between the density or cover of outplanted corals and the density of fishes, regardless of fish size or life stage (Appendix 15), and consequently no change in herbivory or the density of invertebrate corallivores. Although restoration increased overall coral cover ~3 to 12%, our findings suggest that at such low levels of initial coral cover (<2%) this increase may be insufficient to initiate positive feedbacks. Thus, while current restoration

efforts in the Upper Florida Keys have successfully increased the density of *A. cervicornis*, these restored populations may still be at densities too low to foster facilitative interactions between corals and fishes.

Restoration Implications and Recommendations

As the worldwide decline of coral reefs continues (Hughes et al. 2017), the need for effective restoration methods is becoming increasingly urgent (Ladd et al. 2018). Coral restoration has rapidly developed to meet this challenge, evidenced by the success of coral outplanting substantially enhancing populations of targeted coral species (Miller et al. 2016). However, our data suggests that generating community-wide benefits from coral restoration will likely require additional considerations beyond solely outplanting corals. While the primary goal of coral restoration has been to augment coral populations, it is worth considering how future restoration efforts can enhance coral populations in a way that helps kickstart positive feedbacks to facilitate ecosystem functions. Assessing how coral restoration influences major drivers of community dynamics on coral reefs, such as herbivory, corallivory, and disease, will help improve the development of effective restoration strategies. In a time of frequent and intense stress events on reefs across the globe (Hughes et al. 2017, 2018), hastening the speed at which reefs recover critical ecological functions that can promote resistance and resilience to stress events is increasingly important to prevent reoccurring decline on restored reefs.

For example, while outplant survival and growth can be maximized by outplanting at moderate densities (Ladd et al. 2016), finding ways to achieve higher densities of restored coral could benefit restoration by aggregating fishes and initiating positive feedbacks

(Huntington et al. 2017). Beyond promoting coral growth and herbivory (Shantz et al. 2015), concentrating schooling fishes like grunts in restored areas could increase the abundance of fishes that prey on corallivores (Ladd & Shantz 2016), potentially helping to reduce the high incidence of partial mortality and disease we observed in restored areas. Further, leveraging the inverse relationship between predator biomass and damselfish abundance shown for some areas of the Caribbean (Vermeij et al. 2015) could inform restoration site selection.

Outplanting corals at sites with abundant piscivorous fishes, and presumably higher rates of predation on small fishes, could help impinge on the multiple mechanisms by which damselfish may impede coral recovery (Schopmeyer & Lirman 2015).

However, restoring structure alone may not be sufficient to jumpstart recovery on degraded reefs. For instance, Komyakova et al. (2013) found that variation in fish abundance and diversity at Lizard Island on the Great Barrier Reef was mainly due to coral species richness rather than topographic complexity. Promisingly, as coral propagation techniques improve, more species are becoming available for outplanting that may elicit stronger responses in the fish community. Outplanting mixed-species assemblages could reduce the negative impacts of corallivory by deterring the attraction of *C. abbreviata*, which prefer foraging in monospecific patches of *A. cervicornis* (Johnston & Miller 2014). Thus, future work assessing the influence of outplant diversity on restoration outcomes will be important for improving our ability to restore degraded reefs.

Moving forward, restoration efforts that both augment coral populations and promote ecological processes that foster important positive feedbacks can maximize the benefits gleaned from the time, effort, and money invested in restoration, and will also be essential for restoring reefs resilient to future perturbations. However, to do so we must begin to transition

towards incorporating community dynamics and ecosystem processes into restoration planning (Shaver & Silliman 2017; Ladd et al. 2018). Thus, there is a pressing need to develop approaches that restore key processes and functions on coral reefs in order to execute effective and sustainable ecological restoration on coral reefs.

E. Acknowledgements

This work was conducted under Florida Keys National Marine Sanctuary permit no. FKNMS-2014-062. AAS was funded by a DEA grant from FIU. MCL was supported by a grant from the National Science Foundation, Biological Oceanography program (OCE-1130786) to DEB. We thank A. Durán, L. Shaver, S. Csik, and C. Fuchs for assistance in the field and M. Miller for providing feedback that improved the manuscript. The authors have no conflict of interest to declare.

F. References

- Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC, Bernardi G (2011) Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. *PLoS ONE* 6:e23717
- Almany GR (2004) Does increasing habitat complexity reduce predation and competition in coral reef fish assemblages? *Oikos* 106:275–284
- Baums I, Miller M, Szmant A (2003) Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. II. Feeding, respiration and growth. *Marine Biology* 142:1093–1101
- Bayraktarov E, Saunders MI, Abdullah S, Mills M, Behr J, Possingham HP, et al. (2016) The cost and feasibility of marine coastal restoration. *Ecological Applications* 26:1055–

- Bohnsack J, Harper (1988) Length-weight relationships of selected marine reef fishes from the southeastern United States and the Caribbean. Technical Memorandum 215. Miami, Florida, USA.
- Bruno JF, Selig ER (2007) Regional decline of coral cover in the Indo-Pacific: timing, extent, and subregional comparisons. *PloS ONE* 2:e711
- Burke L, Maidens J (2004) *Reefs at Risk in the Caribbean*. Washington, D.C.
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *Proceedings of the National Academy of Sciences of the United States of America* 105:16201–6
- Burkepile DE, Hay ME (2006) Herbivore vs. nutrient control of marine primary producers: context-dependent effects. *Ecology* 87:3128–39
- Catano LB, Gunn BK, Kelley MC, Burkepile DE (2015) Predation risk, resource quality, and reef structural complexity shape territoriality in a coral reef herbivore. *PLoS One* 10:e0118764. doi: 10.1371/journal.pone.0118764
- Catano LB, Barton MB, Boswell KM, Burkepile DE (2017) Predator identity and time of day interact to shape the risk–reward trade-off for herbivorous coral reef fishes. *Oecologia* 183:763–773
- Ferrario F, Beck MW, Storlazzi CD, Micheli F, Shepard CC, Airoidi L (2014) The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nature Communications* 5:3794
- Fox J, Weisberg D, Bates M (2012) Package ‘car’.
- Graham NAJ (2014) Habitat complexity: Coral structural loss leads to fisheries declines.

Current Biology 24:R359–R361

Grorud-Colvert K, Sponaugle S (2009) Larval supply and juvenile recruitment of coral reef fishes to marine reserves and non-reserves of the upper Florida Keys, USA. *Marine Biology* 156:277–288

de Groot R, Brander L, van der Ploeg S, Costanza R, Bernard F, Braat L, et al. (2012) Global estimates of the value of ecosystems and their services in monetary units. *Ecosystem Services* 1:50–61

Hoegh-Guldberg O, Mumby PJ, Hooten AJ, Steneck RS, Greenfield P, Gomez E, et al. (2007) Coral reefs under rapid climate change and ocean acidification. *Science* 318:1737–1742

Holbrook SJ, Forrester GE, Schmitt RJ (2000) Spatial patterns in abundance of a damselfish reflect availability of suitable habitat. *Oecologia* 122:109–120

Hothorn T, Bretz F, Westfall P (2008) Simultaneous inference in general parametric models. *Biometrical Journal* 50:346–363

Hughes TP, Kerry JT, Álvarez-Noriega M, Álvarez-Romero JG, Anderson KD, Baird AH, et al. (2017) Global warming and recurrent mass bleaching of corals. *Nature* 543:373–377

Hughes TP, Anderson KD, Connolly SR, Heron SF, Kerry JT, Lough JM, et al. (2018) Spatial and temporal patterns of mass bleaching of corals in the Anthropocene. *Science* 359:80–83

Huntington BE, Miller MW, Pauch R, Richer L (2017) Facilitation in Caribbean coral reefs: high densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia* 184:247–257

Jackson JBC, Donovan M, Cramer K, Lam V (2014) Status and Trends of Caribbean Coral

- Reefs : 1970-2012. Global Coral Reef Monitoring Network, IUCN, Gland, Switzerland
- Johnston L, Miller MW (2014) Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs* 33:1047–1056
- Jones KMM (2007) Distribution of behaviours and species interactions within home range contours in five Caribbean reef fish species (Family Labridae). *Environmental Biology of Fishes* 80:35–49
- Kiel C, Huntington B, Miller M (2012) Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. *Endangered Species Research* 19:171–176
- Komyakova V, Munday PL, Jones GP (2013) Relative importance of coral cover, habitat complexity and diversity in determining the structure of reef fish communities. *PLoS ONE* 8:1–12
- Ladd MC, Collado-Vides L (2013) Practical applications of monitoring results to improve managing for coral reef resilience: a case study in the Mexican Caribbean. *Biodiversity and Conservation* 22:1591–1608
- Ladd MC, Miller MW, Hunt JW, Sharp WC, Burkepile DE (2018) Harnessing ecological processes to facilitate coral restoration. *Frontiers in Ecology and the Environment* 16:239–247
- Ladd MC, Shantz AA (2016) Novel enemies – previously unknown predators of the bearded fireworm. *Frontiers in Ecology and the Environment* 14:342–343
- Ladd MC, Shantz AA, Nedimyer K, Burkepile DE (2016) Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Frontiers in Marine Science* 3:261

- Lewis SM (1986) The role of herbivorous fishes in the organization of a Caribbean reef community. *Ecological Monographs* 56:183–200
- Lirman D, Schopmeyer S (2016) Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ* 4:e2597
- Lokrantz J, Nyström, Thyresson M, Johansson C (2008) The non-linear relationship between body size and function in parrotfishes. *Coral Reefs* 27:967–974
- Marks KW, Klomp KD (2003) Fish biomass conversion equations. *Atoll Research Bulletin* 496:625–630
- McCook L, Jompa J, Diaz-Pulido G (2001) Competition between corals and algae on coral reefs: a review of evidence and mechanisms. *Coral Reefs* 19:400–417
- Miller MW, Kerr K, Williams DE (2016) Reef-scale trends in Florida *Acropora* spp. abundance and the effects of population enhancement. *PeerJ* 4:e2523
- Montoya-Maya PH, Smit KP, Burt AJ, Frias-Torres S (2016) Large-scale coral reef restoration could assist natural recovery: a case study in Seychelles, Indian Ocean. *Nature Conservation* 16:1–17
- Mumby PJ (2009) Phase shifts and the stability of macroalgal communities on Caribbean coral reefs. *Coral Reefs* 28:761–773
- Mumby PJ, Steneck RS (2008) Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology & Evolution* 23:555–63
- Mumby PJ, Wabnitz CC (2002) Spatial patterns of aggression, territory size, and harem size in five sympatric Caribbean parrotfish species. *Environ Biol Fishes* 63:265–279
- Ogden JC, Quinn TP (1984) Migration in coral reef fishes: Ecological significance and orientation mechanisms. *Mech Migr fishes* 293–308. doi: 10.1007/978-1-4613-2763-

- Oksanen J, Blanchet GF, Friendly M, Kindt R, Legendre P, McGlinn D, et al (2018) *vegan: Community Ecology Package*
- Palmer MA, Filoso S (2009) Restoration of ecosystem services for environmental markets. *Science* 325:575–576
- Pinheiro J, Bates D, DebRoy S, Sarkar D (2015) *nlme: Linear and Nonlinear Mixed Effects Models*.
- R Core Team (2016) *R: A Language and Environment for Statistical Computing*.
- Reaka-Kudla ML (2005) *Biodiversity of Caribbean Coral Reefs*. DesTech Publishers, Lancaster
- Risk A (1998) The effects of interactions with reef residents on the settlement. *Environmental Biology of Fishes* 51:377–389
- Ritson-Williams R, Arnold SN, Fogarty ND, Steneck RS, Vermiej MJA, Paul VJ (2009) New perspectives on ecological mechanisms affecting coral recruitment on reefs. *Smithsonian Contributions to the Marine Sciences* 437–457
- Rotjan R, Lewis S (2008) Impact of coral predators on tropical reefs. *Marine Ecology Progress Series* 367:73–91
- Schopmeyer SA, Lirman D (2015) Occupation dynamics and impacts of damselfish territoriality on recovering populations of the threatened staghorn coral, *Acropora cervicornis*. *PLoS ONE* 10
- Society for Ecological Restoration (SER) (2004) *The SER International primer on ecological restoration*. Tuscon, AZ
- Shantz AA, Ladd MC, Schrack E, Burkepile DE (2015) Fish-derived nutrient hotspots shape

- coral reef benthic communities. *Ecological Applications* 25:2142-2152
- Shaver EC, Burkepile DE, Silliman BR (2018) Local management actions can increase coral resilience to thermally-induced bleaching. *Nature Ecology and Evolution* 2:1075–1079
- Shaver EC, Silliman BR (2017) Time to cash in on positive interactions for coral restoration. *Peer J* e3499:0–30
- Sponaugle S, Lee T, Kourafalou V, Pinkard D (2005) Florida Current frontal eddies and the settlement of coral reef fishes. *Limnology and Oceanography* 50:1033–1048
- Syms C, Jones G (2000) Disturbance, habitat structure, and the dynamics of a coral-reef fish community. *Ecology* 81:2714–2729
- Vermeij M, deBey H, Grimsditch G, Brown J, Obura D, DeLeon R, Sandin SA (2015) Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Marine Ecology Progress Series* 528:289–296
- Williams D, Miller M (2005) Coral disease outbreak: Pattern, prevalence and transmission in *Acropora cervicornis*. *Marine Ecology Progress Series* 301:119–128
- Williams ID, Polunin NVC, Hendrick VJ (2001) Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Marine Ecology Progress Series* 222:187–196
- Young C, Schopmeyer S, Lirman D (2012) A Review of Reef Restoration and Coral Propagation Using the Threatened Genus *Acropora* in the Caribbean and Western Atlantic. *Bulletin of Marine Science* 88:1075–1098
- Zaneveld JR, Burkpile DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, et al. (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nature Communications* 7:11833

V. Harnessing ecological processes to facilitate coral restoration

With Margaret W. Miller, John J. Hunt, William Sharp, and Deron E. Burkepile

Reprinted by permission from John Wiley and Sons: Ladd, M.C., Miller, M.W., Hunt, J.H., Sharp, W. and Burkepile D.E. 2018. Harnessing ecological processes to facilitate coral reef restoration. *Frontiers in Ecology and the Environment*. 16(4): 239-247.

A. Introduction

Although coral reefs cover only <0.1% of Earth's surface, they house more than 30% of total marine biodiversity (Reaka-Kudla 2005), are a key source of fisheries production (Moberg and Folke 1999), and provide shoreline protection for >100 million people living next to coastlines (Ferrario *et al.* 2014). However, corals are in rapid decline on many reefs due to global stressors associated with climate change, such as increasing sea surface temperatures that cause coral bleaching and disease, as well as local stressors such as nutrient pollution, sedimentation, and overfishing (Hughes *et al.* 2017). In the Pacific Ocean, reefs have lost nearly half of their corals over the past four decades (Bruno and Selig 2007) and many have lost an additional 30-50% during the recent (2014-16) global coral bleaching event (Hughes *et al.* 2017). This alarming trend is even more pronounced in the western Atlantic Ocean (henceforth, the Caribbean), where coral reefs have lost approximately 80% of their corals since the mid 1970's (Jackson *et al.* 2014). Although the causes of coral decline are numerous, many of drivers of coral loss are localized, acute disturbances, making coral restoration a feasible method to restore corals in many of areas.

Coral restoration is an increasingly necessary tool to confront declines in coral populations worldwide. Currently, these restoration efforts focus on outplanting nursery-raised corals to augment coral populations with the goal of restoring key foundational species on degraded reefs. These efforts have become increasingly successful at reestablishing target corals that are often threatened or endangered (Young *et al.* 2012; Figure 1). In the Caribbean alone, there are currently more than 150 coral propagation operations in over 20 countries containing tens of thousands of nursery-raised corals for restoration (Lirman and

Schopmeyer 2016). Thus, the nascent field of coral restoration is now on the threshold of conducting substantial restoration programs.

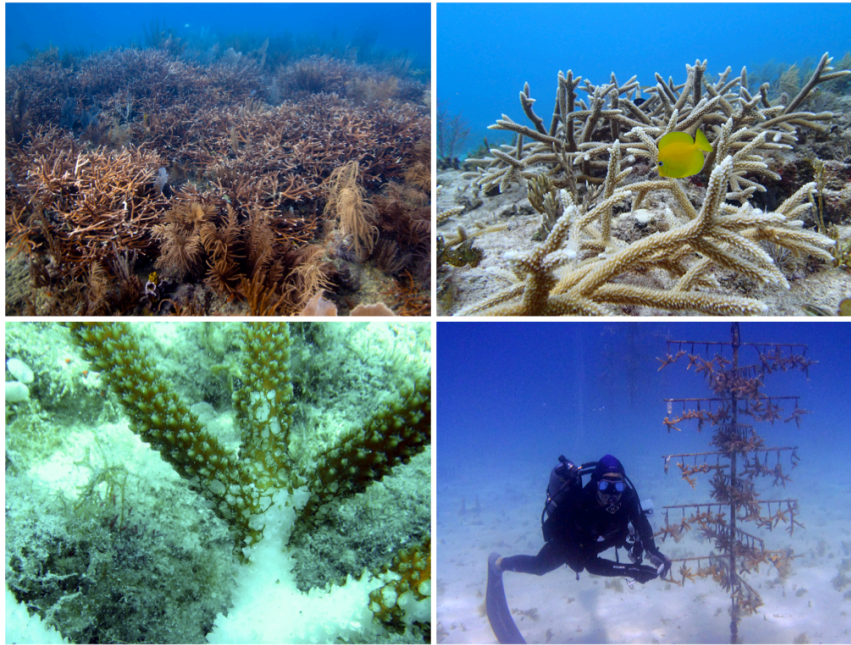


Figure 1. Examples of coral restoration efforts in the Caribbean and western Atlantic. Clockwise from top left: corals outplanted on a degraded reef in Puerto Rico (Courtesy of Sean Griffin, NOAA); juvenile blue tang (*Acanthurus coeruleus*) sheltering within restored *Acropora cervicornis* colonies; coral nursery in the Florida Keys, USA; restored *A. cervicornis* colony displaying signs of rapid tissue loss.

Restoration efforts commonly focus on restoring populations of foundation species that provide the physical structure upon which community members depend for shelter, resources, or reproduction (e.g., grasses; Werner *et al.* 2016; trees; Elliott *et al.* 2003; mangroves; Bosire *et al.* 2008; seagrass; Reynolds *et al.* 2013). There is a long history of restoring foundation species in terrestrial systems where planting trees has been central to restoring key ecosystem processes and services (Holl 2017). However, beyond simply restoring foundation species, restoration efforts often incorporate fundamental ecological processes, such as competition, succession, and herbivory, to restore communities that support important ecosystem functions (Suding *et al.* 2004). Indeed, two decades ago Palmer *et al.* (1997) recognized the central role that basic ecological theory and community ecology

play in effective restoration. For example, manipulating community dynamics by outplanting later successional species is often used to accelerate the process of community succession in restoring terrestrial systems (Palmer *et al.* 1997; Werner *et al.* 2016). Facilitation of target restoration species using nurse plants or specific early successional species is frequently utilized in restoration of terrestrial and coastal ecosystems to reduce physical stress and improve local growing conditions (Bruno *et al.* 2003; Silliman *et al.* 2015).

The practice of harnessing positive interactions and ecological processes to facilitate restoration in terrestrial systems is increasingly being applied to restore degraded aquatic and marine communities (Bruno *et al.* 2003; Halpern *et al.* 2007). For example, promoting genetic diversity in large-scale seagrass restoration planning can restore genetically diverse populations more than an order of magnitude faster than natural regeneration via recruitment (Reynolds *et al.* 2013). Silliman *et al.* (2015) proposed that simple changes in coastal wetland restoration designs that leverage positive interactions, rather than trying to minimize negative ones, can greatly increase restoration success.

While facilitation and ecological processes are often incorporated into restoration approaches in many terrestrial, aquatic, and marine systems, restoration on coral reefs appears slower to embrace this approach. To assess the degree to which ecological processes are incorporated into restoration efforts on coral reefs, we surveyed 116 published scientific papers on coral restoration published from 1987-2017 (Appendix 17). The majority of these studies focused on factors such as the growth and survivorship of corals either in nurseries or outplanted to reefs. Only 19% of the studies incorporated any aspect of ecological processes (e.g. recruitment, predation, herbivory; Table 1).

General Topic	Specific Topic	No. Publications
NURSERY STUDIES (n=45) 39%	Propagation	34
	Growth and survivorship	30
	Genotype traits	10
	Species traits	9
	Site characteristics/effects	5
	Nursery maintenance	3
OUTPLANT STUDIES (n=70) 60%	Attachment method/substrate	23
	Outplant survivorship	58
	Outplant growth	35
	Genotype traits	10
	Species traits	8
RESTORATION DESIGN STUDIES (n=14) 12%	Density	7
	Genotypic diversity	1
	Mixed-species assemblages	5
	Removing macroalgae	1
TESTED OR MEASURED AN ECOLOGICAL PROCESS (n=22) 19%	Recruitment/reproduction	6
	Succession	6
	Predation	5
	Herbivory	3
	Fish-derived nutrients	2
	Disease	1
	Competition	0

Table 1. Number of peer-reviewed articles published on coral restoration and coral reef restoration (1987 – 2017) broken down by the general topic addressed in each study. Publications were categorized by general topic, and then reviewed for the specific topics addressed within each study. Some publications were included in multiple general topics. Percentages represent the percent of publications under a general topic out of the 116 publications reviewed. Search criteria, references for included publications, and category descriptions can be found in Appendix 17.

Additionally, we surveyed 21 coral restoration practitioners conducting coral restoration operations in 12 different countries and territories throughout the Caribbean region to ascertain what factors influence how practitioners choose reefs to conduct coral restoration

and determine sites within those reefs to outplant corals (Table 2; Appendix 18). The three most important factors identified when selecting a reef to conduct restoration were: existing coral cover, available clean substrate, and water depth. Factors associated with ecological processes were generally low on the ranking list.

Yet, when selecting where to outplant corals within a reef, practitioners appeared to give ecological processes more consideration as the three most important factors identified were: outplanting on the best available substrate, avoiding potential benthic competitors, and outplant near herbivores. However, there appears to be little data addressing how effective these different processes may be for facilitating restoration. For example, avoiding benthic competitors was the second most highly ranked criteria for selecting sites to outplant corals (Table 2). Yet, there have been zero scientific studies examining the impacts of competition on restored corals (Table 1). Further, recruitment of fishes and corals has been the most studied process in the context of this restoration (but only 5% of all restoration studies). However, these studies typically only measure recruitment following coral outplanting with little consideration of how the design of restoration can facilitate or impede recruitment. Thus, there is clearly interest in integrating ecological processes into coral restoration, however it is not clear how extensively ecological theory has shaped current practices.

Here, we outline a framework suggesting how restoration practitioners could potentially increase the success and rate of restoration by better integration of key ecological processes such as herbivory, competition, predation, and nutrient cycling into restoration efforts. We propose that restoration practitioners can manipulate where, when, and how corals are outplanted to enhance coral survivorship and growth in order to restore positive or break negative feedback processes. Further, we highlight important knowledge gaps regarding the

ecological underpinnings of coral restoration that need to be addressed with rigorous scientific studies (Appendix 19). By explicitly incorporating methods that either take advantage of or manipulate key processes, restoration efforts may be able to utilize dynamic ecological forces to help hasten the recovery of coral populations.

Rank	Criteria For Selecting Among Reef Locations	Criteria For Selecting Sites Within a Reef
1	Existing coral cover	Outplant on best available substrate
2	Available clean substrate	Avoid potential benthic competitors
3	Water depth	Outplant near herbivores
4	Presence of potential benthic competitors	Ensure corals are distributed throughout restoration site
5	Presence of herbivorous fishes	Outplant close to any existing coral
6	Abundance of coral predators	Avoid coral predators such as corallivorous snails
7	Level of human visitation	Outplant near fish aggregations
8	Presence of algal-farming damselfish	Outplant far from existing coral

Table 2. Rankings of priority given by restoration practitioners to criteria considered when selecting reefs at which to conduct coral outplanting (among reefs) and placement of corals at sites within a reef. Results are from a survey of coral restoration practitioners (n = 21) representing 13 affiliations conducting coral restoration operations in 17 different countries and territories in the Caribbean region.

B. Capitalizing on Important Ecological Processes on Coral Reefs

Promoting Herbivory in Restored Areas

Herbivory by fishes and urchins is one of the strongest forces influencing benthic community structure on coral reefs (Adam *et al.* 2015). Restoration practitioners recognize the importance of herbivory as ‘outplanting near herbivores’ was the third ranked criteria for selecting sites on a reef to outplant corals (Table 2). Yet only 2.5% of studies on coral restoration address herbivory at all, with only one study focusing on herbivory by fishes or urchins. Thus, capitalizing on herbivory in concert with coral restoration, either by outplanting coral in areas where herbivory is high or promoting herbivory on reefs where it is

diminished should be both a research and restoration priority. Herbivory is a linchpin of a series of positive feedbacks that reinforce topographically-complex, coral-dominated reefs thereby supporting ecosystem function (Mumby and Steneck 2008). Robust herbivore populations can suppress macroalgal cover, minimize coral-algal competition, increase coral growth and recruitment, and help coral populations recover after disturbances (Graham *et al.* 2015; Zaneveld *et al.* 2016).

Whereas populations of small coral-associated fish often decline with losses in coral cover, populations of larger, roving fishes such as herbivorous parrotfishes and surgeonfishes may persist in the immediate aftermath of coral loss (Graham *et al.* 2007). For example, in Moorea, French Polynesia, herbivorous fish populations around the island increased after an outbreak of coral-eating sea stars consumed virtually all existing live corals. The increased herbivory facilitated recovery by keeping the substrate free of macroalgae, allowing corals to recruit back to these reefs (Holbrook *et al.* 2016). For reefs with lower coral recruitment rates, restoring corals shortly after an acute disturbance may harness the benefits of existing herbivore populations to help jump-start recovery of coral populations as compared to a site where herbivory is less strong.

Additionally, restoring corals soon after disturbances could help maintain robust herbivorous fish populations as fish larvae, as well as coral larvae, are positively attracted to waterborne chemical cues from corals (Dixon *et al.* 2014). Thus, quickly restoring corals after disturbances might help prevent diminished recruitment of important fishes and corals in the absence of abundant coral. Initiation of such recruitment cascades could hasten the recovery not only of coral populations, but organisms that provide key ecosystem functions such as herbivory and nutrient cycling (e.g. Halpern *et al.* 2007). Such a scenario highlights

the key aspects that larger-scale processes, such as connectivity between reefs and larval supply dynamics, will play in coral restoration planning.

Different types of herbivores likely vary in their ability to facilitate restoration given that herbivores differ in the spatial extent and intensity at which they graze. Urchins can provide a concentrated source of grazing over a small area of the reef ($\sim 1 \text{ m}^2$), whereas herbivorous fishes may provide a more diffuse (100's m^2) source of grazing (Sandin and McNamara 2012). The consistent and intense herbivory provided by urchins can decrease coral-algal competition and allow transplanted or juvenile corals to establish (Sandin and McNamara 2012). Indeed, localized recovery of the historically abundant grazer, the long-spined urchin (*Diadema antillarum*), on some Caribbean reefs have significantly reduced macroalgal cover and increased coral recruitment compared to adjacent areas where *Diadema* are not present (Carpenter and Edmunds 2006).

Establishing recovery nuclei is common in forest restoration to attract community members such as birds and rodents that can deposit seeds, concentrate nutrients, and facilitate succession (Holl 2017). On reefs, restoring coral in areas with existing urchin populations could harness a consistent source of herbivory to facilitate coral growth and serve as recovery nuclei within a degraded reef. However, it remains important to consider the density-dependent nature of urchin benefits; at high densities grazing by urchins can dislodge juvenile corals, kill coral recruits, and reduce the cover of important coral settlement substrate (McClanahan *et al.* 1996). At high densities, or in the absence of adequate coral growth, urchins may work against long-term restoration goals by degrading reef framework (Kuffner and Toth 2016).

Decreasing the amount of substrate open for algal colonization can force herbivores to graze more intensely on remaining space (Williams *et al.* 2001). This might be achieved by increasing the density of corals outplanted for restoration, using fast growing species, and/or corals with morphologies that occupy relatively large amounts of surface area (Figure 2).

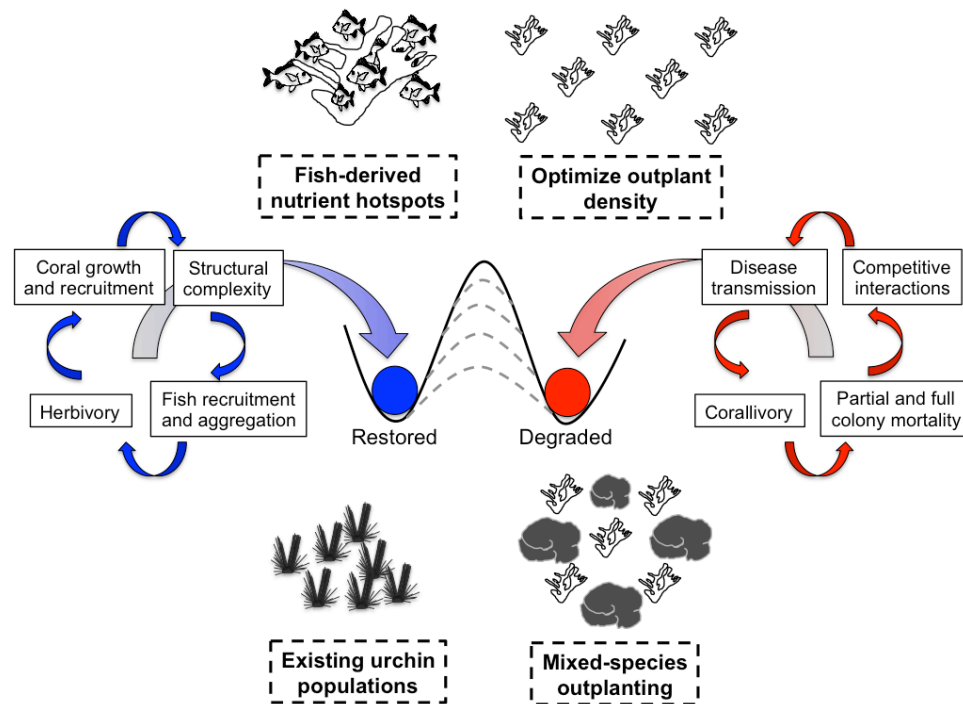


Figure 2. Recovery of corals on a degraded reef can be facilitated by positive feedbacks (center left; modified from Mumby and Steneck 2008). If restoration can promote one or several of these feedback mechanisms, the likelihood for coral recovery increases. Simultaneously, a series of negative feedback mechanisms can operate to inhibit recovery (center right). However, restoration can be designed to impinge on one or multiple negative mechanisms to break these feedbacks and initiate recovery. For example, areas of existing aggregations of fishes could be selected within a site to outplant corals and capitalize on rapid nutrient cycling to promote coral growth (top left). Similarly, outplanting corals to areas within a reef that contain robust populations of herbivorous urchins can take advantage of intense and consistent herbivory to promote coral growth and survival (bottom left). The density of corals outplanted for restoration is a fundamental component that can be tailored to minimize competition, coral mortality, and maximize habitat production (top right). The density of corals likely influences key processes like competition, disease transmission, and the attraction of corallivores, all of which can work against restoration efforts. Mixed-species outplanting could benefit restoration beyond increased species diversity. Using corals that can rapidly occupy the benthos can decrease the amount of grazable substrate available, effectively intensifying herbivory in remaining areas (bottom right).

Additionally, the temporary use of uncolonizable, algal-free surfaces to reduce grazable substrate can concentrate existing herbivory (Williams *et al.* 2001). Coupling targeted high-density outplanting of corals with the re-stocking of grazers such as urchins or parrotfishes

could jumpstart positive feedbacks and hasten the development of recovery nuclei (Maciá *et al.* 2007; Obolski *et al.* 2016). Such approaches may be more feasible for discrete areas such as patch reefs where natural barriers aid in spatially restricting herbivores. *Reducing Coral*

Predation and Disease

Coral predation (i.e., corallivory) is a chronic source of tissue loss and mortality for many species of coral (Rotjan and Lewis 2008). Common predators of coral include invertebrates such as snails, fireworms, and sea stars, as well as damselfishes, butterflyfishes, and other corallivorous fishes. Before the mass bleaching of 2014-16 (Hughes *et al.* 2017), over 40% of the coral cover lost in the past three decades on Australia's Great Barrier Reef is attributed to outbreaks of the corallivorous crown-of-thorns sea star (*Acanthaster planci*; De'ath *et al.* 2012). In the Caribbean, algal-farming damselfishes can be a substantial source of partial mortality for colonies of staghorn coral (*Acropora cervicornis*) outplanted for coral restoration (Schopmeyer and Lirman 2015; Figure 3). Surprisingly, our survey revealed that avoiding or managing corallivory is one of the least important criteria when selecting sites to outplant corals (Table 2), although corallivory seems to have garnered more focus in published coral restoration literature (Table 1). Importantly, there appears to be relatively easy decisions practitioners could make to help minimize predation on restored corals.

As coral cover declines, predation by roving corallivorous fishes can generate an alarming pattern in which predation intensity on corals increases as coral cover decreases (Burkepile 2012). Corallivory from less mobile organisms (e.g. invertebrates) also intensifies as coral cover decreases and food resources become scarcer (Baums *et al.* 2003). Given this relationship, sites with the lowest coral cover may actually be poor choices for restoration,

particularly if the corals being used for restoration are frequent targets of corallivores. Thus, outplanting on reefs with some existing coral populations may be important to reduce damage from corallivory.

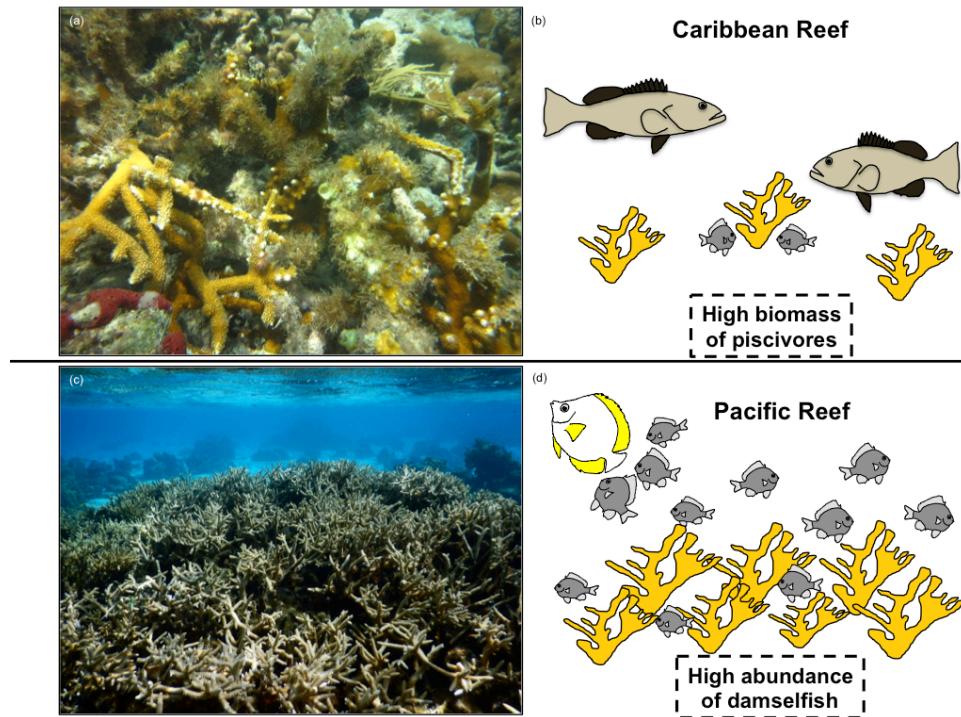


Figure 3. Context-dependent nature of damselfishes in coral reef restoration. Algal garden created by *Stegastes planifrons* on restored *Acropora cervicornis* colonies in the Florida Keys (3a; Courtesy of S. Schopmeyer, University of Miami RSMAS). In the Caribbean, coral reef restoration efforts would likely benefit from choosing sites with high biomass of piscivores to reduce the abundance of damselfish and their negative impacts on corals (3b). Extensive *Acropora* spp. thicket within *Stegastes nigricans* territories on a patch reef in Moorea, French Polynesia (3c; Courtesy of B. Banka, UC Santa Barbara). On reefs in the Indo-Pacific, coral restoration efforts may benefit from targeting areas with a high abundance of territorial damselfishes to reduce predation on corals from roving corallivorous fishes (3d).

Asymmetry in prey preference can also make the outplanting of rare but preferred corals particularly problematic. Such is the case for *A. cervicornis*, the primary species used for coral restoration in the Caribbean, which is the highly-preferred prey of the corallivorous short coral snail (*Coralliophila abbreviata*; Johnston and Miller 2014). In regions with high spatial variability of corallivore abundance, avoiding reefs with large populations of

corallivores in favor of targeting sites with low corallivore abundance could help to stymie this negative feedback hindering coral restoration (Williams *et al.* 2014).

Current restoration efforts largely focus on restoring one or a few species of corals. However, as coral propagation techniques advance, the increasing number and diversity of corals available for restoration affords the opportunity to test and employ creative approaches to restoration. Some coral species, such as *Porites* spp. in the Caribbean (Miller and Hay 1998) and *Acropora* spp. and *Montipora* spp. in the Pacific (White and O'Donnell 2010) are rapidly consumed when transplanted onto a reef. Limiting access by corallivores to palatable coral species by protecting them with less palatable branching corals is one creative approach to reduce corallivory and increase the diversity of corals being restored. In Florida, colonies of *A. cervicornis* outplanted next to conspecifics were more rapidly preyed upon compared to those outplanted next to different species (Johnston and Miller 2014). Similarly, colonies of the leaf coral (*Pavona frondifera*) outplanted next to finger corals (*Porites cylindrica*) suffered lower predation rates than *P. frondifera* outplanted with conspecifics (Cabaitan *et al.* 2015). If the corals being used for restoration are heavily targeted by corallivores, informed use of mixed-species assemblages of corals may help reduce the attraction of corallivores and their negative effects on coral restoration (Figure 2). Such an approach would parallel positive interactions commonly utilized in terrestrial restoration (Bruno *et al.* 2003).

Coral disease is a significant source of mortality that can have devastating effects on coral populations (Precht *et al.* 2016). Although we did not ask about disease specifically in our survey of practitioners, our literature search surprisingly showed that only one study out of 116 has focused on disease dynamics in restored corals (Table 1). There is a clear mismatch here between the importance of disease as a source of coral mortality and the level

of focus it has received in published restoration studies. Many corallivores may vector disease among corals, including species used for restoration (Williams and Miller 2005). For example, the bearded fireworm (*Hermodice carunculata*), a voracious coral predator and a reservoir for coral disease (Sussman *et al.* 2003), frequently consumes *A. cervicornis* (Miller *et al.* 2014). Competition between corals and the common green alga *Halimeda opuntia* can attract *H. carunculata*, increasing the prevalence of coral disease and coral mortality (Wolf and Nugues 2013). Thus, seeking ways to control both algal competition (such as restoring areas with abundant fishes and/or urchins) and coral predators may aid in reducing coral diseases.

Fishes and other reef inhabitants that prey on corallivores represent potential biological controls that could be leveraged to facilitate restoration. For example, white grunts (*Haemulon plumierii*), a fish common on Caribbean reefs, readily consume adult *H. carunculata* (Ladd and Shantz 2016), while the carnivorous deltoid rock snail (*Thais deltoidea*) preys on the corallivore *C. abbreviata* (Sharp and Delgado 2015), which can also vector coral diseases (Williams and Miller 2005). Restoring corals in areas with abundant *H. plumierii* or *T. deltoidea* may help suppress the negative impacts of corallivores.

Alternatively, deployment of structures that increase the recruitment or aggregation of fishes like *H. plumierii* or actively seeding restoration areas with *T. deltoidea* could help reduce the abundance of corallivores and transmission of coral diseases in restored areas.

Algal-Farming Fishes as Context-Dependent Forces in Coral Restoration

Processes that impact coral survivorship, and ultimately restoration efforts, may be context-dependent. For example, many damselfishes are territorial algal-gardeners that could

promote or hinder restoration efforts depending on geographic location and species-specific behavior (Figure 3). In the Caribbean, territorial damselfishes (e.g. *Stegastes planifrons*) kill large portions of live coral tissue to create algal gardens that are fiercely protected from larger herbivores (Rotjan and Lewis 2008). *Stegastes planifrons* can rapidly colonize colonies of *A. cervicornis* outplanted for restoration, cause significant amounts of partial colony mortality (Schopmeyer and Lirman 2015; Figure 3a), and may increase the prevalence of coral disease (Vermeij *et al.* 2015). Thus, coral restoration efforts should avoid areas with large damselfish populations. Further, concentrating coral outplants to areas with high biomass of piscivorous fishes may reduce the abundance of damselfishes and their negative impact on corals (Figure 3b).

Conversely, on Indo-Pacific reefs, territories of the common damselfish *Stegastes nigricans* can promote the survival and growth of rare corals that are otherwise rapidly consumed by corallivorous fishes (White and O'Donnell 2010). The corals within these territories are often fast-growing, branching species (e.g. *Acropora* spp.) amenable for use in restoration (White and O'Donnell 2010; Figure 3c). Restoration efforts on reefs with abundant *S. nigricans* and other similar damselfish species may benefit from focusing coral outplanting within damselfish territories to facilitate the growth and recruitment of corals and act as nuclei of recovery. Particularly in areas with robust corallivore populations, the protection provided by farming damselfishes such as *S. nigricans* may be crucial for the initial growth and establishment of corals outplanted for restoration (Figure 3d).

Fish-derived Nutrients Promote Positive Feedbacks for Corals

The structure provided by living corals can aggregate fishes and concentrate fish-derived nutrients that increase coral growth (Holbrook *et al.* 2008). These fish-derived nutrient hotspots also increase grazing by herbivorous fishes and decrease algal abundance, both of which likely help facilitate coral growth and survivorship (Shantz *et al.* 2015). Additionally, many of the fishes that aggregate around structurally complex corals are invertivores, such as *H. plumierii*, potentially promoting top-down control on coral predators (Ladd and Shantz 2016). Fish-derived nutrient hotspots appear to both facilitate the growth of existing corals and concentrate herbivory such that the resultant benthic communities also promote coral health and recruitment.

These natural positive feedbacks on coral health may be important to capture in coral restoration designs, yet such processes and feedbacks are not typically part of coral restoration approaches (Tables 1 & 2). Fish-derived nutrient hotspots promote many of the processes central to reef recovery (e.g. herbivory, coral growth, habitat production, coral recruitment). Further, many of the coral species that are commonly used for restoration (e.g. *Acropora* spp., *Pocillopora* spp.) benefit most strongly from fish-derived nutrients. Focusing coral outplanting to sites of existing fish aggregations, or capitalizing on positive density-dependence of corals used for restoration to maximize habitat production and facilitate the aggregation of fishes could harness these positive feedbacks to drive coral reef recovery (Figure 2).

Competition in the Context of Restoration

Competition for limiting resources can drive population dynamics, community succession, and ecosystem function (Hillerislambers *et al.* 2012), particularly on coral reefs where space is a highly-contested resource (Chadwick and Morrow 2011). On many reefs, weedy, fast growing species, such as sponges and soft corals are replacing reef-building corals (Norström *et al.* 2009) and slowing the growth and survivorship of remaining corals (Chadwick and Morrow 2011). Thus, frequent and abundant competitive interactions can generate a series of negative feedbacks that can inhibit the regeneration of diverse, topographically complex coral reefs and impede restoration efforts.

Understanding competitive interactions among corals used for restoration and their benthic competitors could assist in restoration site selection, as practitioners are clearly interested in avoiding benthic competitors when outplanting corals (Table 2). Yet, there have been no studies to date examining how competition impacts coral restoration (Table 1), making this an area ripe for new research (Appendix 19). Within sites, outplanting corals to avoid superior competitors presents a relatively simple method to improve coral growth and survival. On Caribbean reefs, the encrusting gorgonian *Erythropodium caribaeorum* and the zoanthid *Palythoa caribaeorum* are two aggressive, fast growing species that can kill or suppress the growth of *A. cervicornis* (Karlson 1980; Suchanek and Green 1981). Removing these competitors when outplanting *A. cervicornis* or targeting outplants to areas with a low abundance of these competitors could reduce or eliminate one factor working against restoration efforts.

C. Future Directions and Concluding Remarks

Translating ecological theory into realistic approaches for conservation practitioners is one of the most challenging aspects of ecological restoration (Figure 2). Promoting positive density dependent processes to facilitate restoration is a fundamental component of terrestrial and aquatic restoration planning (Halpern *et al.* 2007). For example, outplanting grasses in high densities can promote pollination, increase seed set, and hasten the recovery of grasslands (Morgan and Scacco 2006). Outplanting salt marsh plants in high densities can reduce abiotic stress, increase biomass production, and initiate facilitation cascades (Silliman *et al.* 2015). On coral reefs, the density of corals outplanted is a basic element of restoration planning that may drive many of the ecological processes that will ultimately determine restoration success (Figure 2). For example, outplanting *A. cervicornis* at moderate densities can promote positive density dependence that maximizes habitat production and minimizes coral mortality (Ladd *et al.* 2016). Meanwhile, outplanting at higher densities can invoke negative density-dependent processes that reduce coral growth and survivorship, possibly by attracting coral enemies such as corallivores or facilitating disease (Ladd *et al.* 2016). Such findings highlight the important role density likely plays in the rate and success of coral reef recovery.

However, we lack fundamental knowledge on the mechanisms driving density dependence and how abiotic and biological context can mediate the strength and direction of density dependence. Although many restoration practitioners currently consider density in their restoration design (Table 2), the fact that targeted coral densities varied more than two orders of magnitude (0.1-25 corals m⁻²) highlights the need for a better mechanistic understanding of density dependence among corals to optimize restoration efforts. One such

scenario would be identifying if disease transmission drives negative density dependence in high-density outplants. If this mechanism were confirmed, genotypes resistant to disease (Vollmer and Kline 2008) might facilitate successful outplanting at higher densities to hasten habitat production without increased risk of disease transmission. The potentially key role of density in restoration success underscores the need for further work to understand patterns and drivers of density dependence in species used for coral restoration.

Corals vary widely in basic traits that can drive population and community structure such as growth rates, reproductive output, and symbiont identity that vary among species, populations, and individuals within a population (Madin *et al.* 2016). Initial research has shown significant variability among nursery-raised genotypes for traits such as growth and branching rates (e.g. Lirman *et al.* 2014). For coral restoration, knowledge of important traits of corals used for restoration would allow restoration practitioners to select species and genotypes best suited for specific restoration sites (Elliot *et al.* 2003). For example, at sites frequently impacted by thermal stress, weighting the corals outplanted for restoration towards genotypes of corals known to exhibit high thermal tolerance could better prepare the site for future thermal anomalies (Ladd *et al.* 2017). Matching coral traits with the environment of a restoration site could maximize the survival of outplanted corals and make restoration efforts more effective and efficient. Yet, there remains a paucity of data on inter- and intraspecific differences in many traits relevant to coral restoration and, particularly, their potential ecological tradeoffs (Sandel *et al.* 2011). Although the process of gathering data on these traits may be time consuming and expensive, the ability to make trait-based selections of corals informed by data, while maintaining overall genotypic diversity, would provide restoration practitioners a valuable tool to increase restoration efficacy.

Considerable progress has been made in the past decade in the field of coral restoration. However, many important questions remain unanswered, slowing our ability to restore these key foundation species (Appendix 19). As corals continue their decline around the world, it is urgent we address these questions. Testing and refining innovative, non-traditional approaches to restoring corals, such as harnessing important ecological processes, is an important next step to advance the field of coral restoration ecology. However, addressing these critical questions to better understand how to restore corals is necessary, but not sufficient, to ensure the persistence of corals and coral reefs. In addition to these restoration efforts, we must also make progress to reduce local sources of coral mortality such as pollution and sedimentation as well as reduce carbon emissions to lower the rate and extent of climate change. Without the dual efforts of coral restoration and stress mitigation, corals and coral reefs face a dire future.

D. Acknowledgements

We thank the Florida Fish and Wildlife Conservation Commission (FWC) and the US Fish and Wildlife Service (USFWS) State Wildlife Grants Program for funding a series of workshops to identify many of the research needs for coral reef ecosystem restoration reviewed in this article (State Wildlife Grant Award F13AF01085). We thank A. Bourque, E McDevitt, T Moore, J Walczak, and A Whittle, who, along with the authors, served on the steering committee for the workshop and A Acosta, A Baker, W Fitt, I Enochs, K Erickson, C Frankenfeld, D Gilliam, A Johnson, J Landsberg, E Larson, E Lipp, D Lirman, M Matz, K Maxwell, E Muller, J Parkinson, V Paul, E Peters, B Reckenbeil, R Ruzicka, S Schopmeyer,

L Toth, S Vollmer, and C Woodley for their participation in the workshop. Special thanks to M Truglio of FWC's Wildlife Legacy Initiative.

E. References

- Adam TC, Burkepile DE, Ruttenberg BI, and Paddock MJ. 2015. Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar Ecol Prog Ser* **520**: 1–20.
- Baums IB, Miller MW, and Szmant AM. 2003. Ecology of a corallivorous gastropod, *Coralliophila abbreviata*, on two scleractinian hosts. I: population structure of snails and corals. *Mar Biol* **142**: 1083–91.
- Bosire JO, Dahdouh-Guebas F, Walton M, *et al.* 2008. Functionality of restored mangroves: a review. *Aquat Bot* **89**: 251–9.
- Bruno JF, Stachowicz JJ, and Bertness MD. 2003. Inclusion of facilitation into ecological theory. *Trends Ecol Evol* **18**: 119–25.
- Bruno JF, Selig ER, Casey KS, *et al.* 2007. Thermal stress and coral cover as drivers of coral disease outbreaks. *PLoS Biol* **5**: 1220–7.
- Burkepile DE. 2012. Context-dependent corallivory by parrotfishes in a Caribbean reef ecosystem. *Coral Reefs* **31**: 111–20.
- Chadwick NE and Morrow KM. 2011. Competition among sessile organisms on coral reefs. In: Dubinsky Z, Stambler N (Eds). *Coral Reefs: An Ecosystem in Transition*. Dordrecht: Springer Netherlands.
- Cabaitan PC, Yap HT, and Gomez ED. 2015. Performance of single versus mixed coral species for transplantation to restore degraded reefs. *Restor Ecol* **23**: 1–8.

- De'ath G, Fabricius KE, Sweatman H, and Puotinen M. 2012. The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proc Natl Acad Sci* **109**: 17995–9.
- Dixson DL, Abrego D, and Hay ME. 2014. Chemically mediated behavior of recruiting corals and fishes: A tipping point that may limit reef recovery. *Science* **345**: 892–7.
- Elliott S, Navakitbumrung P, Kuarak C, *et al.* 2003. Selecting framework tree species for restoring seasonally dry tropical forests in northern Thailand based on field performance. *For Ecol Manage* **184**: 177–91.
- Ferrario F, Beck MW, Storlazzi CD, *et al.* 2014. The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nat Commun* **5**: 3794.
- Graham NAJ, Jennings S, MacNeil MA, *et al.* 2015. Predicting climate-driven regime shifts versus rebound potential in coral reefs. *Nature* **518**: 1–17.
- Graham NAJ, Wilson SK, Jennings S, *et al.* 2007. Lag effects in the impacts of mass coral bleaching on coral reef fish, fisheries, and ecosystems. *Conserv Biol* **21**: 1291–300.
- Halpern B, Silliman B, Olden J, *et al.* 2007. Incorporating positive interactions in aquatic restoration and conservation. *Front Ecol Environ* **5**: 153–60.
- Hillerislambers J, Adler PB, Harpole WS, *et al.* 2012. Rethinking community assembly through the lens of coexistence theory. *Annu Rev Ecol Evol Syst* **43**: 227–48.
- Holbrook SJ, Brooks AJ, Schmitt RJ, and Stewart HL. 2008. Effects of sheltering fish on growth of their host corals. *Mar Biol* **155**: 521–30.
- Holbrook SJ, Schmitt RJ, Adam TC, and Brooks AJ. 2016. Coral reef resilience, tipping points and the strength of herbivory. *Sci Rep* **6**: 35817.
- Holl KD. 2017. Restoring tropical forests from the bottom up. *Science* **355**: 455–6.
- Hughes TP, Kerry J, Álvarez-Noriega M, *et al.* 2017. Global warming and recurrent mass

- bleaching of corals. *Nature* **543**: 373–7.
- Hughes TP, Barnes ML, Bellwood DR, *et al.* 2017. Coral reefs in the Anthropocene. *Nature* **546**: 82-90.
- Jackson JBC, Donovan MK, Cramer KL, and Lam W. 2014. Status and trends of Caribbean coral reefs : 1970-2012. Gland, Switzerland: Global Coral Reef Monitoring Network, IUCN.
- Johnston L and Miller MW. 2014. Negative indirect effects of neighbors on imperiled scleractinian corals. *Coral Reefs* **33**: 1047–56.
- Karlson R. 1980. Alternative competitive strategies in a periodically disturbed habitat. *Bull Mar Sci* **30**: 894–900.
- Kuffner IB and Toth LT. 2016. A geological perspective on the degradation and conservation of western Atlantic coral reefs. *Conserv Biol* **30**: 706–15.
- Ladd MC and Shantz AA. 2016. Novel enemies – previously unknown predators of the bearded fireworm. *Front Ecol Environ* **14**: 342–3.
- Ladd MC, Shantz AA, Nedimyer K, and Burkepile DE. 2016. Density dependence drives habitat production and survivorship of *Acropora cervicornis* used for restoration on a Caribbean coral reef. *Front Mar Sci* **3**: 1–14.
- Ladd MC, Shantz AA, Bartels E, and Burkepile DE. 2017. Thermal stress reveals a genotype-specific tradeoff between growth and tissue loss in restored *Acropora cervicornis*. *Mar Ecol Prog Ser* **572**: 129–39.
- Lirman D and Schopmeyer S. 2016. Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ* **4**: e2597.
- Lirman D, Schopmeyer S, Galvan V, *et al.* 2014. Growth dynamics of the threatened

- Caribbean Staghorn coral *Acropora cervicornis*: influence of host genotype, symbiont identity, colony size, and environmental setting. *PLoS One* **9**: e107253.
- Maciá S, Robinson MP, and Nalevanko A. 2007. Experimental dispersal of recovering *Diadema antillarum* increases grazing intensity and reduces macroalgal abundance on a coral reef. *Mar Ecol Prog Ser* **348**: 173–82.
- Madin JS, Hoogenboom MO, Connolly SR, *et al.* 2016. A trait-based approach to advance coral reef science. *Trends Ecol Evol* **31**: 419–28.
- Miller MW and Hay ME. 1998. Effects of fish predation and seaweed competition on the survival and growth of corals. *Oecologia*: 231–8.
- Miller MW, Marmet C, Cameron CM, and Williams DE. 2014. Prevalence, consequences, and mitigation of fireworm predation on endangered staghorn coral. *Mar Ecol Prog Ser* **13**: 226–7.
- Moberg F and Folke C. 1999. Ecological goods and services of coral reef ecosystems. *Ecol Econ* **29**: 215–33.
- Morgan JW and Scacco PJ. 2006. Planting designs in ecological restoration: insights from the Button Wrinklewort. *Ecol Manag Restor* **7**: 51–4.
- Mumby PJ and Steneck RS. 2008. Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends Ecol Evol* **23**: 555–63.
- Norström A, Nyström M, Lokrantz J, and Folke C. 2009. Alternative states on coral reefs: beyond coral–macroalgal phase shifts. *Mar Ecol Prog Ser* **376**: 295–306.
- Obolski U, Hadany L, and Abelson A. 2016. Potential contribution of fish restocking to the recovery of deteriorated coral reefs: an alternative restoration method? *PeerJ* **4**: e1732.
- Palmer AP, Ambrose RF, and Poff NL. 1997. Ecological theory and community restoration

- ecology. *Restor Ecol* **5**: 291-300.
- Precht WF, Gintert BE, Robbart ML, *et al.* 2016. Unprecedented disease-related coral mortality in southeastern Florida. *Sci Rep* **6**: 31374.
- Reaka-Kudla ML. 2005. Biodiversity of Caribbean coral reefs. Lancaster: DesTech Publishers.
- Reynolds LK, Waycott M, and McGlathery KJ. 2013. Restoration recovers population structure and landscape genetic connectivity in a dispersal-limited ecosystem.
- Rotjan R and Lewis S. 2008. Impact of coral predators on tropical reefs. *Mar Ecol Prog Ser* **367**: 73–91.
- Ruzicka R, Colella M, Porter J, *et al.* 2013. Temporal changes in benthic assemblages on Florida Keys reefs 11 years after the 1997/1998 El Niño. *Mar Ecol Prog Ser* **489**: 125–41.
- Sandel B, Corbin JD, and Krupa M. 2011. Using plant functional traits to guide restoration: A case study in California coastal grassland. *Ecosphere* **2**: 1–16.
- Sandin SA and McNamara DE. 2012. Spatial dynamics of benthic competition on coral reefs. *Oecologia* **168**: 1079–90.
- Schopmeyer SA and Lirman D. 2015. Occupation dynamics and impacts of damselfish territoriality on recovering populations of the threatened staghorn coral, *Acropora cervicornis*. *PLoS One* **10**.
- Shantz AA, Ladd MC, Shrack E, and Burkepile DE. 2015. Fish-derived nutrient hotspots shape coral reef benthic communities. *Ecol Appl* **25**: 2142–52.
- Sharp WC and Delgado GA. 2015. Predator-prey interactions between the corallivorous snail *Coralliophila abbreviata* and the carnivorous deltoid rock snail *Thais deltoidea*. *Biol Bull*

229: 129–33.

Silliman BR, Schrack E, He Q, *et al.* 2015. Facilitation shifts paradigms and can amplify coastal restoration efforts. *Proc Natl Acad Sci*: 201515297.

Suchanek T and Green D. 1981. Interspecific competition between *Palythoa caribaeorum* and other sessile invertebrates on St. Croix reefs, U.S. Virgin Islands. In: Proc 4th Int Coral Reef Symp.

Suding KN, Gross KL, and Houseman GR. 2004. Alternative states and positive feedbacks in restoration ecology. *Trends Ecol Evol* **19**: 46–53.

Sussman M, Loya Y, Fine M, and Rosenberg E. 2003. The marine fireworm *Hermodice carunculata* is a winter reservoir and spring-summer vector for the coral-bleaching pathogen *Vibrio shiloi*. *Environ Microbiol* **5**: 250–5.

Vermeij M, DeBey H, Grimsditch G, *et al.* 2015. Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Mar Ecol Prog Ser* **528**: 289–96.

Vollmer S V and Kline DI. 2008. Natural disease resistance in threatened staghorn corals. *PLoS One* **3**: e3718.

Werner CM, Vaughn KJ, Stuble KL, *et al.* 2016. Persistent asymmetrical priority effects in a California grassland restoration experiment. *Ecol Appl* **6**: 1624–32.

White J-SS and O'Donnell JL. 2010. Indirect effects of a key ecosystem engineer alter survival and growth of foundation coral species. *Ecology* **91**: 3538–48.

Williams DE and Miller MW. 2005. Coral disease outbreak : pattern, prevalence and transmission in *Acropora cervicornis*. *Mar Ecol Prog Ser* **301**: 119–28.

Williams DE, Miller MW, Bright AJ, and Cameron CM. 2014. Removal of corallivorous

snails as a proactive tool for the conservation of acroporid corals. *PeerJ* **2**: e680.

Williams ID, Polunin NVC, and Hendrick VJ. 2001. Limits to grazing by herbivorous fishes and the impact of low coral cover on macroalgal abundance on a coral reef in Belize. *Mar Ecol Prog Ser* **222**: 187–96.

Wolf AT and Nugues MM. 2013. Synergistic effects of algal overgrowth and corallivory on Caribbean reef-building corals. *Ecology* **94**: 1667–74.

Young C, Schopmeyer S, and Lirman D. 2012. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic. *Bull Mar Sci* **88**: 1075–98.

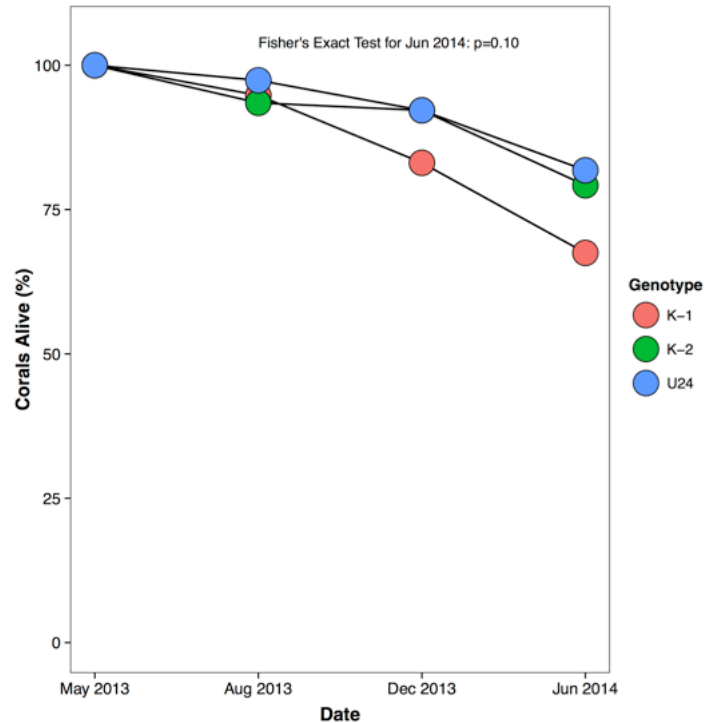
Zaneveld JR, Burkepile DE, Shantz AA, *et al.* 2016. Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* **7**.

Appendices

Appendix 1. Results from nested two-way repeated measures ANOVA for genotype effects on growth rates, TLE, and live TLE.

Response Variable	Predictor	<i>F</i>	<i>P</i>
Growth rate (cm day ⁻¹)	Time	12.677	< 0.001
	Genotype	0.022	0.978
	Genotype x Time	1.087	0.364
Individual colony TLE	Time	268.414	< 0.001
	Genotype	0.267	0.766
	Genotype x Time	0.450	0.845
Individual colony Live TLE	Time	12.047	< 0.001
	Genotype	0.012	0.988
	Genotype x Time	0.363	0.902

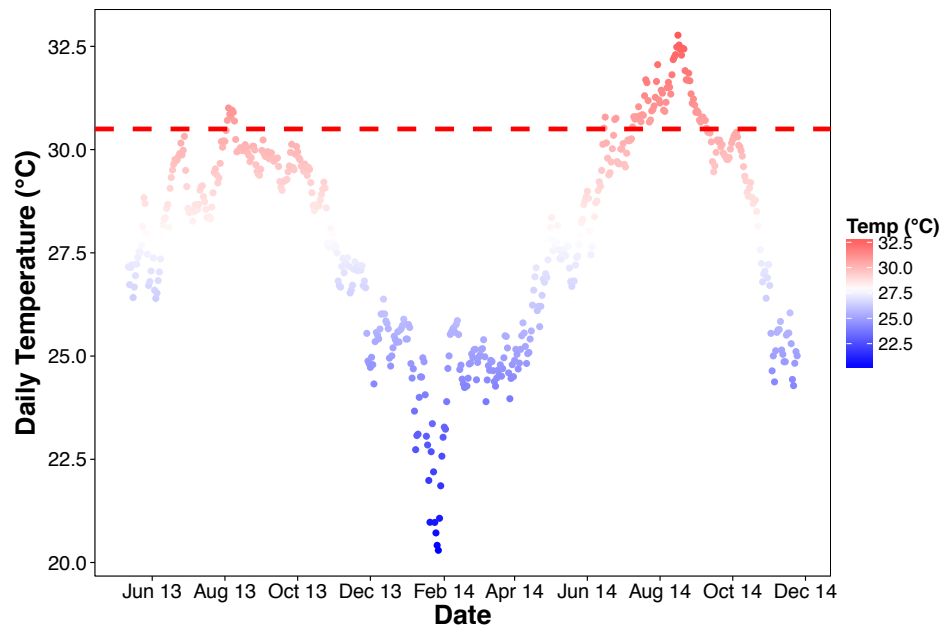
Appendix 2. Survivorship of coral colonies by genotype over time.



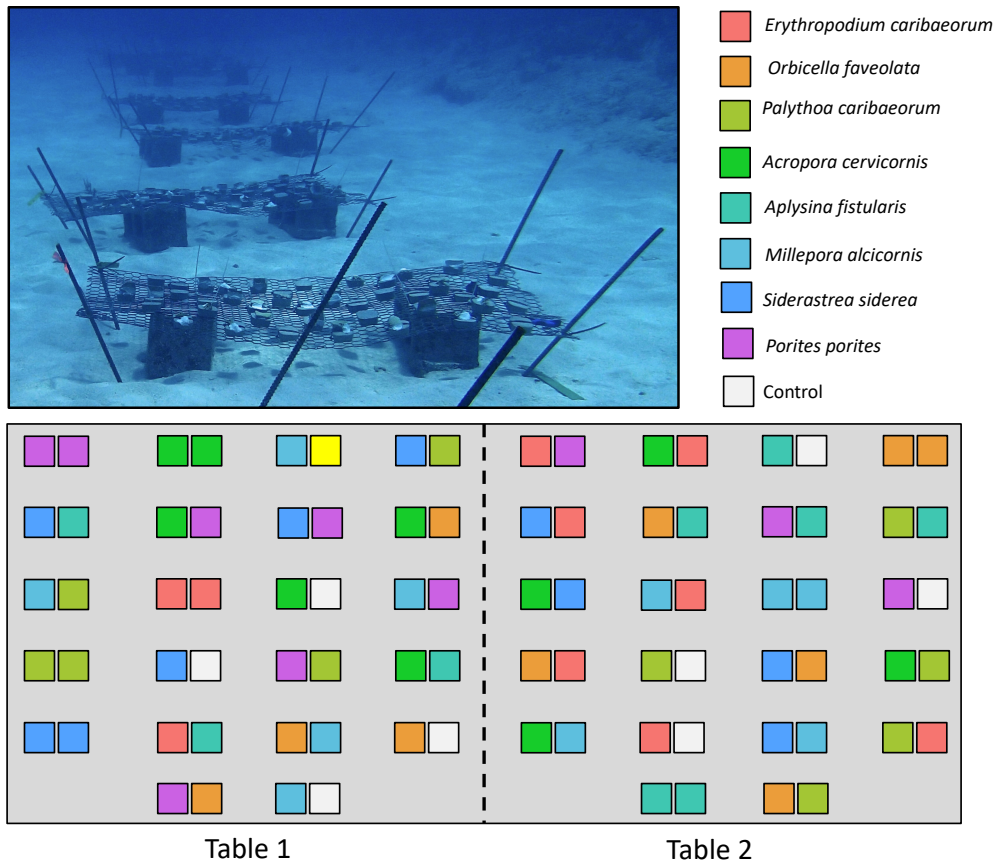
Appendix 3. Results from nested two-way repeated measures ANOVA for treatment effects on individual colony growth rate, TLE, live TLE, and results from two-way ANOVA for plot level TLE, live TLE, and survivorship.

Response Variable	Predictor	df1	df2	F	P
Growth rate (cm day ⁻¹)	Time	2	222	48.144	< 0.001
	Treatment	4	12	2.950	0.065
	Treatment x Time	8	222	4.694	< 0.001
Individual colony TLE	Time	3	476	69.511	< 0.001
	Treatment	4	12	0.495	0.740
	Treatment x Time	12	476	3.960	< 0.001
Individual colony Live TLE	Time	3	476	8.598	< 0.001
	Treatment	4	12	0.082	0.987
	Treatment x Time	12	476	13.322	< 0.001
Plot level TLE	Time	4	60	80.577	< 0.001
	Treatment	3	60	37.906	< 0.001
	Treatment x Time	12	60	1.193	0.309
Plot level live TLE	Time	4	60	24.756	< 0.001
	Treatment	3	60	6.645	< 0.001
	Treatment x Time	12	60	2.240	0.021
Survivorship	Time	4	72	4.108	< 0.001
	Treatment	4	72	24.404	< 0.001
	Treatment x Time	16	72	25.491	< 0.001

Appendix 4. Daily water temperature recorded at a nearby site in the Lower Florida Keys at a similar depth to our experimental site. The red dashed line depicts the bleaching threshold (30.5°C) for *Acorpora cervicornis* according to Manzello *et al.* (2007).



Appendix 5. Photograph of experimental platforms deployed in a sand flat near Pickles Reef (top left). Schematic of one complete replicate of experimental pairs for the common garden competition experiment (not to scale).



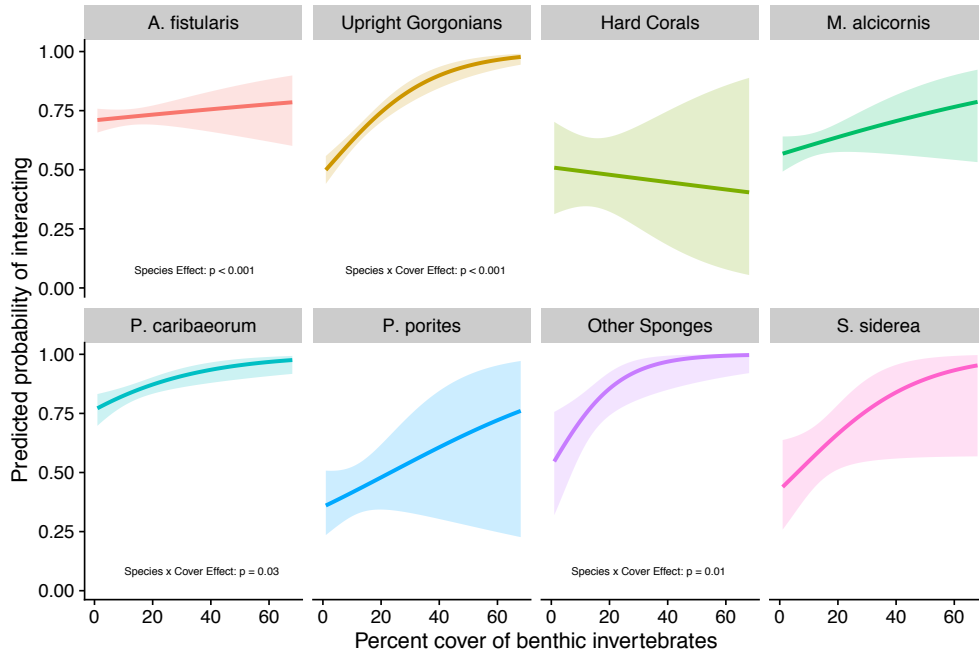
Appendix 6. Descriptions of the 12 benthic categories used for percent cover analysis of photoquadrats. Groups highlighted in grey denote focal species. Groups with an asterisk indicate groups included in our interaction frequency surveys (Figure 1).

Benthic Group	Mean Percent Cover	SE	Description
<i>Aplysina fistularis</i> *	1.34	0.166	Individuals of the focal species <i>Aplysina fistularis</i>
Upright gorgonian*	7.63	0.955	Any erect gorgonian, regardless of species
Hard coral*	0.11	0.039	All non-focal scleractinian species
Macroalgae	9.60	2.110	Fleshy macroalgae
<i>Millepora alcicornis</i> *	0.98	0.276	Individuals of the focal species <i>Millepora alcicornis</i>
Other	2.07	0.504	Non-natural items such as PVC frame, hand, ruler, etc.
<i>Palythoa caribaeorum</i> *	0.62	0.128	Individuals of the focal species <i>Palythoa caribaeorum</i>
<i>Porites porites</i> *	0.07	0.032	Individuals of the focal species <i>Porites porites</i>
Sand	0.17	0.129	Sand
Other Sponge*	0.26	0.080	All sponges except <i>Aplysina fistularis</i>
<i>Siderastrea siderea</i> *	0.14	0.057	Individuals of the focal species <i>Siderastrea siderea</i>
Turf-algal sediment matrix	76.61	3.918	Turf-algal sediment matrix <i>sensu</i> Connell et al. 2014

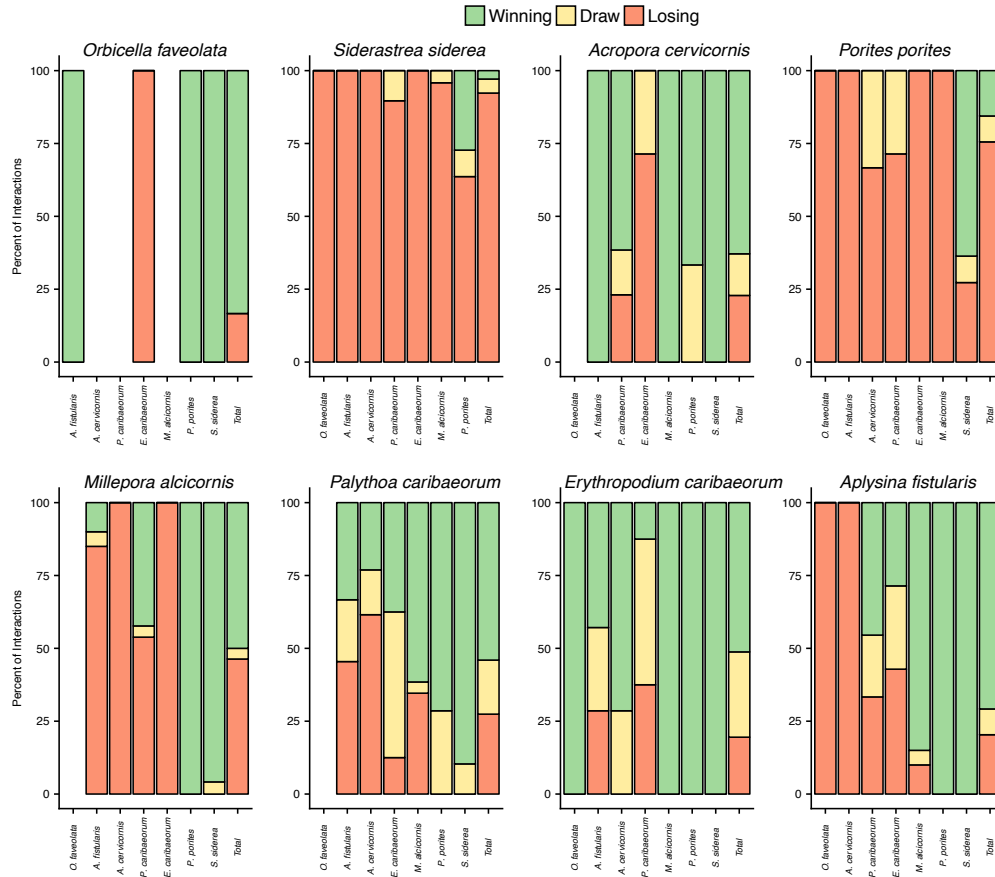
References:

Connell SD, Foster MS, Airoidi L (2014) What are algal turfs? Towards a better description of turfs. *Mar Ecol Prog Ser* 495:299–307

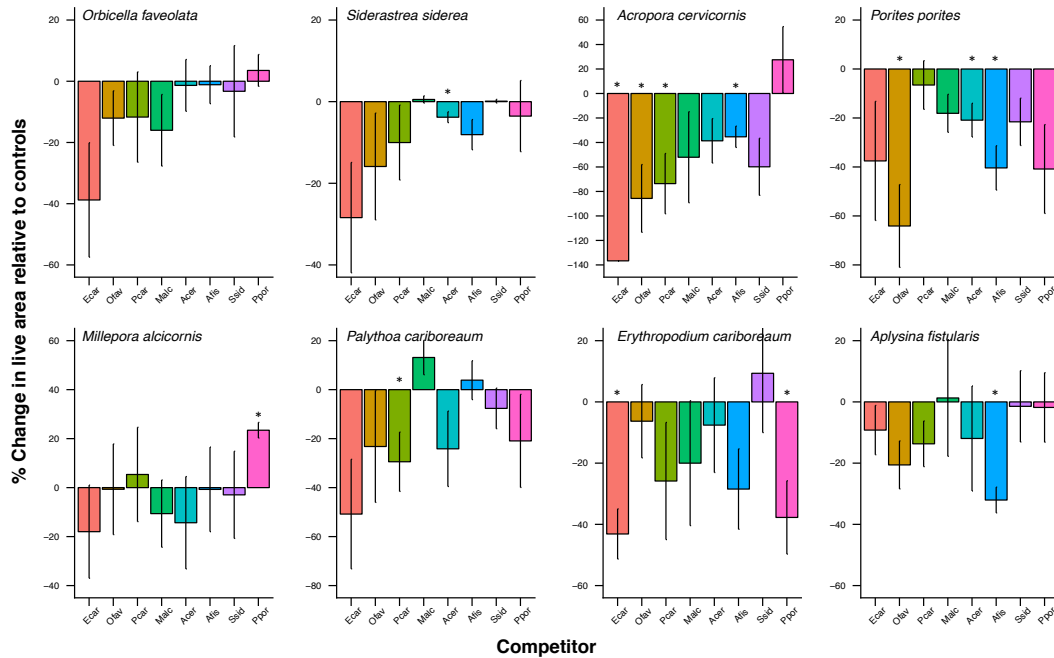
Appendix 7. Predicted probabilities of an individual interacting with increasing percent cover of benthic invertebrates. Statistics are from a linear mixed effects model.



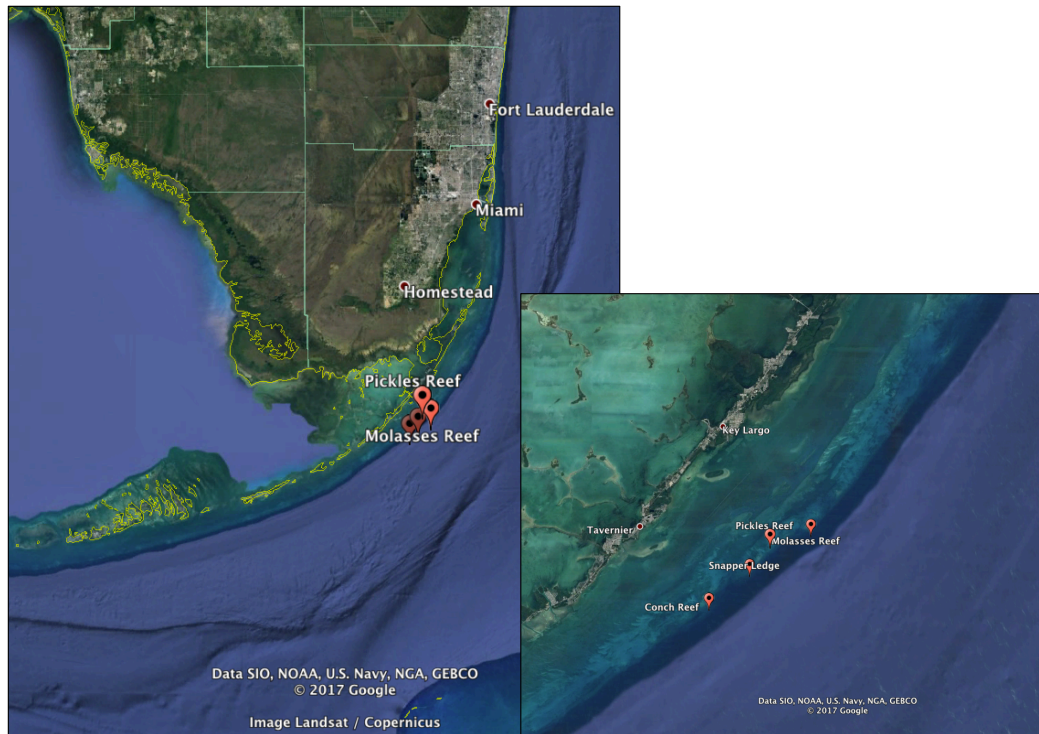
Appendix 8. Species-specific competitive outcomes from field surveys in the summer of 2014 for each of the eight focal species of this study. Numbers at the bottom of each bar represent the sample size for each species-specific pairing.



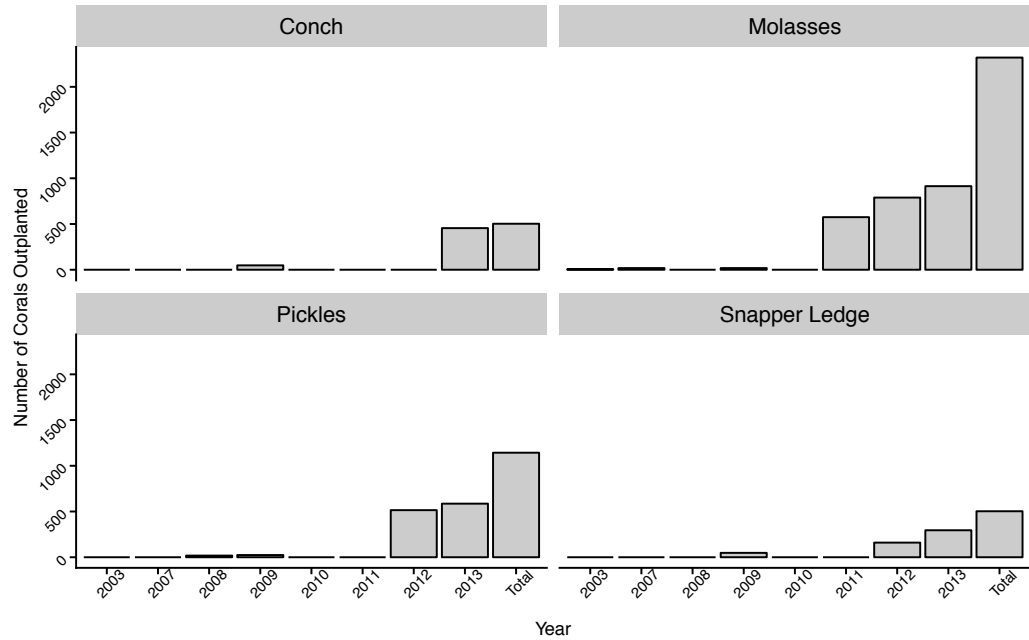
Appendix 9. Mean percent change in live area (July to December) for each species-specific interaction relative to mean change in live area of control individuals, calculated by subtracting the percent change of the control from the percent change of individuals in competition for each species pairing. Asterisks indicate that the 95% confidence interval did not include zero. Data are means \pm SE from the common garden competition experiment. *Orbicella faveolata* data presented are from July to October.



Appendix 10. Locations of the four reefs in the Upper Florida Keys, USA surveyed in this study.



Appendix 11. Number of nursery-raised *Acropora cervicornis* colonies outplanted at each study reef from 2003 to 2013. Outplant data provided by the Coral Restoration Foundation.



Appendix 12. List of all coral species found within control and restored sites. Letters correspond to reefs at which each species was observed (C = Conch Reef, M = Molasses Reef, P = Pickles Reef, SL = Snapper Ledge).

Species	Restored	Control
<i>Acropora cervicornis</i>	C, M, P, SL	M, P, SL
<i>Acropora palmata</i>	SL	M
<i>Agaricia agaricites</i>	C, M, P, SL	C, M, P, SL
<i>Copophylia natans</i>	M	M, SL
<i>Dendrogyra cylindrus</i>		C
<i>Dichocoenia stokesii</i>	C, P, SL	C, M, P, SL
<i>Diploira clivosa</i>	M	M
<i>Diploria labyrinthiformis</i>	M, P, SL	C, SL
<i>Diploria strigosa</i>	P	C
<i>Eusmilia fastigiata</i>	C, M	P, M, SL
<i>Favia fragum</i>	SL	
<i>Madracis decactus</i>	C, M, P, SL	P, M, SL
<i>Madracis formosa</i>	P	
<i>Meandrina jacksonii</i>	SL	C, SL
<i>Meandrina meandrites</i>	P	C, M, P, SL
<i>Montastraea cavernosa</i>	C, M, P, SL	C, M, P, SL
<i>Mycetophyllia ferox</i>	P	
<i>Orbicella faveolata</i>	M, P, C	M, P
<i>Porites astreoides</i>	M, P, SL	C, M, P, SL
<i>Porites furcata/divaricata</i>	C, M, P, SL	M, SL
<i>Porites porites</i>	C, M, P, SL	C, M, P, SL
<i>Siderastrea radians</i>	C, M, SL	C, M, SL
<i>Siderastrea siderea</i>	C, M, P, SL	C, M, P, SL
<i>Solenastrea bournoni</i>	P	P
<i>Stephanocoenia intersepta</i>	C, M, P, SL	C, M, P, SL

Appendix 13. Results from SIMPER analysis. Table displays the ten coral species that contributed most to community dissimilarity in restored vs. control sites, and the percentage of dissimilarity that each species accounted for.

Coral Species	Contribution to Community Dissimilarity
<i>Acropora cervicornis</i>	47.8%
<i>Agaricia</i> spp.	23.5%
<i>Porites porites</i>	9.4%
<i>Siderastrea siderea</i>	6.4%
<i>A. palmata</i>	3.0%
<i>P. astreoides</i>	2.8%
<i>Madracis decactis</i>	1.1%
<i>Dichocoenia stokesi</i>	1.0%
<i>Stephanocoenia intersepta</i>	1.0%
<i>Siderastrea radians</i>	0.6%

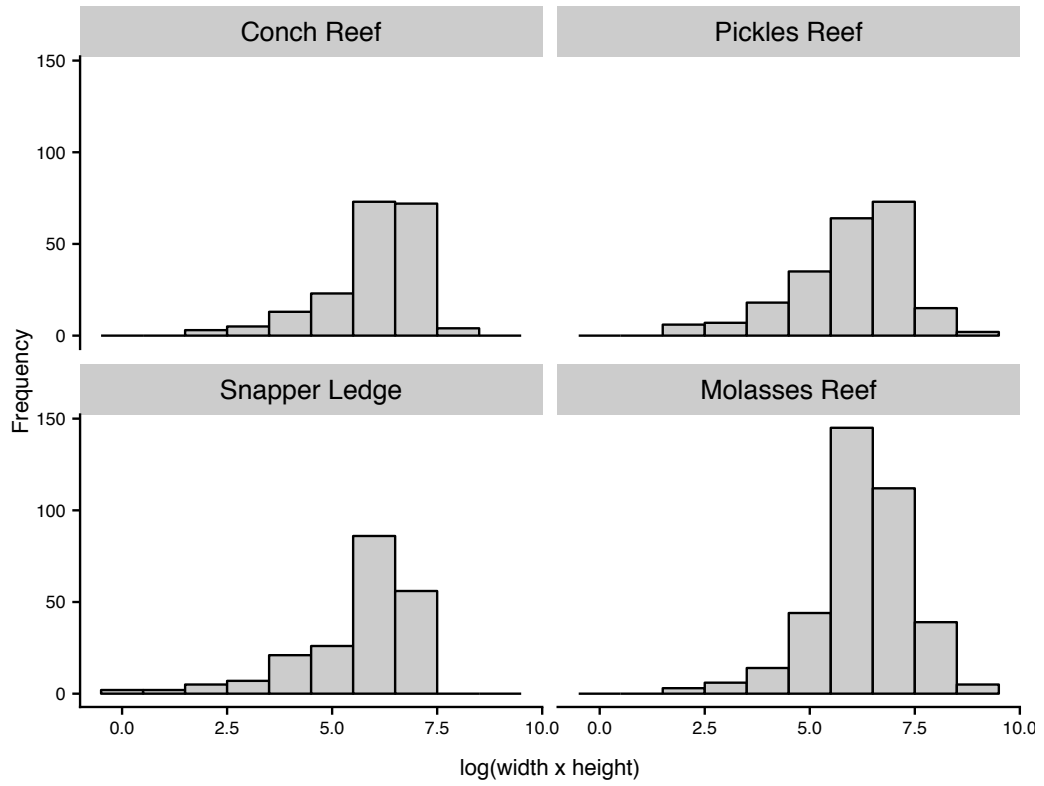
Appendix 14. Results from mixed-effects models testing the effect of Treatment, Reef, and Treatment x Reef interaction on individual functional group biomass and density of fishes. “--” indicates that there were not enough replicates to run the model with interaction.

Fish functional Group	Response variable	Treatment df	Treatment p-value	Site df	Reef p-value	Interaction df	Treatment x Reef p-value
Invertivore	Biomass	1	0.781	3	0.498	3	0.104
	Density	1	0.202	3	0.412	3	0.385
Herbivore	Biomass	1	0.180	3	0.722	3	0.069
	Density	1	0.002	3	0.150	3	0.015
Piscivore	Biomass	1	0.363	3	0.973	3	0.552
	Density	1	0.474	3	0.851	3	0.441
Corallivore	Biomass	1	<0.001	3	0.734	NA	---
	Density	1	0.946	3	0.980	NA	---
Planktivore	Biomass	1	0.918	3	0.996	3	0.960
	Density	1	<0.001	3	0.496	3	0.929

Appendix 15. Results from linear models testing the effect of the density of *A. cervicornis* in cm total TLE m⁻² and restored coral cover (i.e. *Acropora cervicornis* only, fixed factor) on indicators for key ecological processes.

Response variable	Metric	Chi-squared	df	p-value
Snail density	cm TLE m ⁻²	0.339	1	0.561
	<i>A. cervicornis</i> cover	0.567	1	0.452
Percent of seagrass assay consumed	cm TLE m ⁻²	1.859	1	0.173
	<i>A. cervicornis</i> cover	0.728	1	0.394
All fish	cm TLE m ⁻²	1.423	1	0.239
	<i>A. cervicornis</i> cover	1.831	1	0.176
Fish <15cm TL	cm TLE m ⁻²	0.672	1	0.412
	<i>A. cervicornis</i> cover	1.466	1	0.226
Juvenile fish	cm TLE m ⁻²	0.032	1	0.857
	<i>A. cervicornis</i> cover	0.073	1	0.787
Damsel fish	cm TLE m ⁻²	0.351	1	0.553
	<i>A. cervicornis</i> cover	0.451	1	0.502
Partial colony mortality	cm TLE m ⁻²	2.950	1	0.0859
	<i>A. cervicornis</i> cover	3.305	1	0.069
Number of diseased colonies	cm TLE m ⁻²	1.415	1	0.234
	<i>A. cervicornis</i> cover	0.475	1	0.491

Appendix 16. Frequency distribution of the size ($\log_{10}(\text{width} \times \text{length})$) of restored *Acropora cervicornis* surveyed in 2014 within restored sites at each reef.



Appendix 17. Coral restoration and coral reef restoration peer-reviewed literature review

Methods: To conduct a comprehensive search of published literature on coral restoration, we searched ISI Web of Science for “coral restoration”, “coral reef restoration”, “coral transplantation”, and similar terms. We included papers from the time period 1987-2017. We also mined the references of relevant papers, such as recent reviews on coral restoration projects (e.g. Johnson *et al.* 2011; Young *et al.* 2012; Lirman and Schopmeyer 2016). To be included, a publication had to include data from a study focused on corals used for restoration, or conducted some aspect of coral reef restoration (e.g. deployment of artificial substrate to attract coral recruits). Therefore, we did not include publications that were purely modeling, theoretical, or opinions and did not present data. Each publication was reviewed and evaluated based on the below criteria (Table 1). If the criteria were met, the publication was then assessed and assigned to the appropriate “general topics” and “specific topics”. A publication could be assigned to multiple general and/or specific topics if the appropriate criteria were met. In total we found 116 papers that met our criteria.

Table 1. Criteria for “general topics” (gray shaded cells) and “specific topics” (no shading) within each general topic.

Topic	Criteria
Nursery Studies	Studies conducted in a nursery (<i>in-situ</i> or <i>ex-situ</i>) study that included one of the below specific topics
Propagation	Methods for growing corals in a nursery setting (<i>ex-situ</i> or <i>in-situ</i>), including sexual reproduction methodologies.
Growth and survivorship	Measured growth and survivorship of corals in a nursery setting
Genotype traits	Quantified differences in traits (e.g. thermal tolerance) of multiple genotypes of the same species in a nursery setting. Growth rate included as a trait
Species traits	Quantified differences in traits (e.g. thermal tolerance) of multiple species in a nursery setting. Growth rate included as a trait
Site characteristics/effects	Compared growth or survivorship among nursery-raised corals growing in multiple nursery locations with different abiotic characteristics (e.g., depth, water flow, sedimentation)
Nursery maintenance	Methods for maintaining nurseries (e.g. cleaning growth structures)
Outplant Studies	Studies that outplanted corals grown in a nursery and measured one of the following specific topics
Attachment method/substrate	Compared methods for attaching corals to substrate, or measured attachment success of corals outplanted to multiple types of substrate (e.g. sand vs. rubble vs. pavement)
Outplant survivorship	Measured survivorship of corals outplanted to a degraded reef for restoration
Outplant growth	Measured growth rates of corals outplanted to a degraded reef for restoration
Species traits	Measured traits of multiple species of corals outplanted for restoration. Traits included growth rates, thermal tolerance, <i>Symbiodinium</i> density and composition, etc.

Genotype traits	Measured traits of multiple genotypes of the same species of coral outplanted for restoration. Traits included growth rates, thermal tolerance, <i>Symbiodinium</i> density and composition, etc.
Restoration Design Studies	Studies that explicitly test a component of coral restoration outplant design
Density	Tested the effect of the density of corals used for restoration on coral growth, survivorship, or an ecological process of interest (e.g. disease prevalence)
Genotypic diversity	Tested the effect of the genotypic diversity of corals used for restoration on coral growth, survivorship, or response to stress
Mixed-species assemblages	Tested the effect of mixed-species assemblages of corals used for restoration on growth, survivorship, or an ecological process of interest (e.g. predation)
Removing macroalgae	Tested the effect of removing macroalgae on the growth and survivorship of corals used for restoration
Tested or Measured and Ecological Process	Studies that either explicitly tested the influence of an ecological process (herbivory, corallivory, disease, competition, recruitment or reproduction, fish-derived nutrients) on the success of coral restoration or measured how one or several of these ecological process changed as a result of coral restoration
Succession	Measured the development of benthic or fish communities in response to coral restoration
Disease	Quantified how disease impacts corals used for restoration, or methods to minimize the negative effects of disease on corals used for restoration
Predation	Quantified predation rates on corals used for restoration, or methods to mediate predation on corals used for restoration
Recruitment/reproduction	Quantified how restoration (outplanting corals or modifying the substrate/structure of a degraded reef) influences the recruitment of corals. Also included studies that tracked how long it took for corals outplanted for restoration to become sexually mature
Herbivory	Quantified the effect of herbivory on the growth, survivorship, or competitive interactions of corals outplanted for restoration
Fish-derived nutrients	Quantified the effect of fish-derived nutrients on corals outplanted for restoration, herbivory, or benthic community succession
Competition	Tested the effect of intra- or interspecific competition on the growth and survivorship of corals used for restoration

References

Johnson M, Lustic C, Bartels E, *et al.* 2011. Caribbean Acropora Restoration Guide: Best Practices for Propagation and Population Enhancement. Arlington, VA: The Nature

Conservancy.

- Lirman D and Schopmeyer S. 2016. Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ* **4**: e2597.
- McMurray SE and Pawlik JR. 2009. A novel technique for the reattachment of large coral reef sponges. *Restor Ecol* **17**: 192–5.
- Young C, Schopmeyer S, and Lirman D. 2012. A Review of Reef Restoration and Coral Propagation Using the Threatened Genus *Acropora* in the Caribbean and Western Atlantic. *Bull Mar Sci* **88**: 1075–98.

Methods: To quantify contemporary trends and approaches in coral restoration, we developed a survey that asked coral restoration practitioners throughout the Caribbean region a series of questions regarding their restoration activities. We were particularly interested in how practitioners select sites for coral restoration, where corals are outplanted within a site, and any additional factors taken into consideration when planning and conducting restoration activities. The full questionnaire can be found at the end of WebPanel 1. For questions regarding how important specific factors were for restoration efforts, we employed a forced ranking system whereby the participant ranked options 1 through 8 (1 = most important, 8 = least important). This methodology allowed us to quantify the relative importance of each factor in current coral restoration approaches. Responses were analyzed by calculating the average rank given to each factor to determine which were given the highest and lowest priority by restoration practitioners.

We emailed the survey directly to a list of ~60 individuals known to be conducting coral restoration throughout the Caribbean with the intent to maximize the number of organizations and geographic locations (restricted to the Caribbean) surveyed. During the sampling period of 14 days, we received 21 completed surveys (~35% completion rate) from 13 different affiliations (universities, marine labs, US state and federal agencies, NGOs, independent contractor) conducting coral restoration in 17 different countries or territories in the Caribbean region.

Results: Eighty-six percent of participants said they consider density in their outplanting efforts, with target densities ranging from 0.1 to 25 coral colonies m^{-2} (mean \pm SE: 8.0 colonies $m^{-2} \pm 2.6$). Ninety percent of participants identified genotypic diversity as an important component of their restoration planning. Although the majority of participants indicated they try to maximize genotypic diversity at all of their restoration sites, 48% also indicated they select coral genotypes for specific traits when planning coral restoration efforts. However, only 19% actively select corals within their nursery for known performance traits (e.g., tolerance to disease or thermal stress), whereas the remaining 29% use corals that have survived past stress events (i.e., passive selection). No participants said that they select coral genotypes to try to maximize coral growth, and 52% of those surveyed have outplanted mixed-species assemblages.

The three most important factors identified when selecting a site to conduct restoration were: (1) existing coral cover, (2) available clean substrate, and (3) water depth. Factors associated with ecological processes were ranked (4) presence of potential benthic competitors, (5) presence of herbivorous fishes, (6) abundance of coral predators, and (8) presence of algal-farming damselfishes. Other factors that restoration practitioners identified as important to consider when selecting a site for coral restoration included algal cover, disease prevalence, substrate quality, rugosity, distance to other outplants, time of the year (to avoid outplanting during the hot summer months), historical distribution of restoration species, tourism use, and outplant size. When selecting where to outplant corals within a restoration site, the three most important factors identified were: (1) outplanting on the best available substrate, (2) avoiding potential benthic competitors, and (3) outplant near herbivores.

Coral Restoration Practitioner Survey

1. First, tell us about your coral restoration activities. Please mark all of the appropriate activities listed below:

- Maintain in situ nursery
- Maintain ex situ nursery
- Routinely outplant nursery-propagated *Acropora cervicornis*
- Routinely outplant nursery-propagated *Acropora palmata*
- Outplant other species of nursery-propagated corals
- Reattached damaged corals encountered

2. Do you consider outplant density?

- yes/no

3. Do you consider coral genotypic diversity?

- yes/no

4. Have you selected corals to outplant with specific traits to withstand stressors such as temperature, disease, etc.

- yes/no

5. Have you selected coral genotypes to outplant specifically to maximize growth?

- yes/no

6. Have you outplanted mixed coral species assemblages?

- yes/no

7. What other components do you consider when planning coral restoration activities?

8. Below are several potential factors you may consider when selecting a coral restoration site. Please rank these factors in order of importance to you from 1-8. Enter a "1" for your most important factor, a "2" for the next important factor, and so on for the remaining factors. NOTE: no two factors can have the same number.

- Available clean substrate
- Existing coral cover
- Presence of herbivorous fishes
- Water depth
- Level of human visitation
- Presence of potential benthic competitors
- Abundance of coral predators
- Presence of algal-farming damselfish

9. Once a restoration site has been selected, below are several potential approaches you could consider when you are outplanting corals. Please rank these factors in

order of importance to you from 1-8. Enter a "1" for your most important factor, a "2" for the next important factor, and so on for the remaining factors. NOTE: no two factors can have the same number.

- Outplant close to any existing coral
- Outplant far from existing coral
- Avoid potential benthic competitors
- Outplant on best available substrate
- Outplant near herbivores
- Ensure corals are distributed throughout the restoration site
- Avoid coral predators such as corallivorous snails
- Outplant near fish aggregations

10. Please tell us about any other restoration activities you couple with your coral restoration efforts

- Restock herbivorous fishes
- Restock herbivorous urchins
- Deploy surfaces to concentrate herbivory
- Remove coral predators at outplanting
- Remove coral predators after outplanting
- Deploy fish aggregating devices
- Introduce predators
- Other considerations

11. If you remove corallivores for an extended time after outplanting, please tell how often and for how long you continue this activity.

(open question)

12. What do you think are the most important knowledge gaps that need to be addressed to effectively conduct coral reef restoration of ecologically meaningful scales?

(open question)

13. Please tell us in what regions you conduct coral restoration (e.g., Florida, Virgin Islands, etc.)

(open question)

14. Please tell us your affiliation (i.e., your Agency, Organization, University)
(open question)

Appendix 19. Knowledge gaps and research needs that should be addressed to advance the science and efficacy of coral restoration.

<i>Ecological process</i>	<i>Major restoration goals</i>	<i>Research questions to be addressed</i>
Herbivory	<i>Reduce algal abundance</i> <i>Reduce coral-algal interactions</i> <i>Increase coral growth rates</i> <i>Promote conditions favorable for successful coral recruitment</i>	How can the density of corals used for restoration be manipulated to increase rates of herbivory in restored areas?
		How does the density and species of corals used for restoration influence the identity (species, phase, size) of herbivores?
		Can corals with morphologies that occupy lots of surface area be used to increase the intensity of existing herbivory by reducing grazable space?
		Can spatially constrained herbivores such as urchins be restored along with corals to promote recovery?
		Can the use of artificial structures effectively enhance herbivory to facilitate success of restored corals?
Corallivory	<i>Reduce the attraction of corallivores</i> <i>Reduce corallivory densities</i> <i>Reduce partial and full mortality from corallivory</i> <i>Reduce negative secondary effects from corallivory (e.g. disease transmission, dislodgement, etc.)</i>	How does the density of outplanted corals influence the attraction of coral predators?
		How does the density of existing corals or other structural aspects of habitat at a site mediate predation of restored corals?
		What are the primary drivers of corallivore abundance?
		What reef organisms consume corallivores?
		How can restoration aggregate predators of important corallivores?
		What species or genotypes of corals do corallivores prefer?
		What species and genotypes of corals used for restoration are most resistant/resilient to predation?
		How can restoration utilize “natural protection” from corallivory (e.g., damselfish)?
		Can outplanting of multiple coral species be used to reduce attraction or access to preferred coral species?
Disease	<i>Minimize the transmission and extent of coral disease</i>	How does the density of outplanted corals influence disease transmission?
		What species and genotypes of corals used for restoration are resistant to disease infection?
		What ecological tradeoffs exist among important coral traits?

		Can species and/or genotypic diversity enhance resistance to disease?
Competition and Facilitation	<i>Utilize competitive relationships to drive community development</i>	How does the density of corals used for restoration influence coral growth rates, survivorship, and habitat production?
		Can specific assemblages of corals promote growth, survivorship and the generation of habitat?
		Do competitive hierarchies exist that could be used to incorporate succession into restoration planning?
		What benthic competitors should be avoided?
		Are there benthic species that can facilitate the growth and survival of corals used for restoration?
Fish-derived Nutrients	<i>Capitalize on the positive feedback mechanisms stemming from localized delivery of nutrients within a reef</i>	Can the density of restored corals be manipulated to promote the aggregation of fishes that can create nutrient hotspots?
		At what threshold does outplant density promote coral and fish recruitment?
		Can artificial structures foster fish aggregation and the generation of nutrient hotspots early in restoration?
		What coral species being used for restoration are most effective at aggregating fishes that can create nutrient hotspots?