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UNIVERSITY OF CALIFORNIA SAN DIEGO

Effects of Invasive Species Removal and Coral Transplantation on Benthic Community
Structure at Palmyra Atoll

A Thesis submitted in partial satisfaction of the requirements
the degree Master of Science

in

Marine Biology

by

Corinne Galit Amir

Committee in charge:

Professor Jennifer Smith, Chair
Professor Elsa Cleland
Professor Stuart Sandin

2019

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University of California San Diego

2019

TABLE OF CONTENTS

Signature Page	iii
Table of Contents	iv
List of Abbreviations	v
List of Figures	vi
List of Tables	vii
Acknowledgements	viii
Abstract of the Thesis	ix
Introduction.....	1
Methods.....	6
Results.....	15
Discussion.....	19
Conclusion	27
Figures and Tables	29
Appendix.....	42
References.....	48

LIST OF ABBREVIATIONS

CON	No corallimorph removal + no coral transplantation treatment (full control)
REM	Corallimorph removal + no coral transplantation treatment (removal control)
RAN	Corallimorph removal + non-aggregated coral transplantation treatment (random transplantation)
XSP	Corallimorph removal + coral aggregation of mixed species transplantation treatment (cross species transplantation)
BYSP	Corallimorph removal + coral aggregated of same species transplantation treatment (by species transplantation)
CAU	Calcification accretion unit
CPC	Change in percent cover
VPI	Viscore Virtual Point Intercept analysis
ENSO	El Niño—Southern Oscillation
CCA	Crustose coralline algae
Control Treatments	All Treatments without coral transplants (CON and REM)
Transplant Treatments	All treatments containing coral transplants (RAN, XSP, and BYSP)

LIST OF FIGURES

Figure 1.	Schematic of restoration site experimental design	29
Figure 2.	Workflow of Viscore model alignment, scaling, and orientation	30
Figure 3.	Workflow of Viscore Virtual Point Intercept analysis	31
Figure 4.	Images of representative CAU device tile sides following a one-year deployment.....	32
Figure 5.	Percent cover of all coral species, <i>A. acuminata</i> , <i>M. capitata</i> , and <i>P. damicornis</i> from Sept. 2015-Sept. 2018	33
Figure 6.	Change in percent cover from 2015-2018 of each coral transplant species across all treatments	34
Figure 7.	Benthic community composition of each treatment from 2015-2018.....	35
Figure 8.	NMDS plot of the benthic successional trajectories of each treatment from Sept. 2015-Sept. 2018	36
Figure 9.	Results of <i>in situ</i> juvenile coral surveys including mean juveniles per m ² and relative species abundance in Sept. 2017 and Sept. 2018	37
Figure 10.	Relationship between damselfish abundance and coral percent cover, <i>A. acuminata</i> thickets abundance, and corals >5 cm in diameter.....	38
Figure 11.	Results of CAU device community composition, total biomass production rate, reef accretion rate, and non-calcified biomass production rate within each deployment period	39
Figure 12.	Orthophotos of a representative removal + non-aggregated transplants (RAN) treatment in Sept.2015, Jun. 2016, Sept. 2017, and Sept. 2018.....	42
Figure 13.	Orthophotos of a representative removal + transplants aggregated by species (BYSP) treatment in Sept. 2015, Jun. 2016, Sept. 2017, and Sept. 2018.....	43
Figure 14.	Orthophotos of a representative removal + transplants aggregated across species (XSP) treatment in Sept. 2015, Jun. 2016, Sept. 2017, and Sept. 2018.....	44
Figure 15.	Orthophotos of a representative removal + no transplants (REM) treatment in Sept. 2015, Jun. 2016, Sept. 2017, and Sept. 2018.....	45
Figure 16.	Orthophotos of a representative no removal + no transplants (CON) treatment in Sept. 2015, Jun. 2016, Sept. 2017, and Sept. 2018.....	46

LIST OF TABLES

Table 1.	Results of a PERMANOVA testing differences in overall benthic community composition across treatments and across time points.....	40
Table 2.	Results of a PERMANOVA testing differences in CAU community composition across treatments and across time points.....	41

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ABSTRACT OF THE THESIS

Effects of Invasive Species Removal and Coral Transplantation on Benthic Community Structure at Palmyra Atoll

by

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Master of Science in Marine Biology

University of California San Diego, 2019

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Invasive and opportunistic species are known to cause turnovers in dominant taxa by rapidly monopolizing space following disturbance events, often producing lasting shifts in community structure provided that environmental conditions remain favorable. On Palmyra Atoll, the corallimorph *Rhodactis howesii* has become highly invasive and now covers > 3 km² of reef radiating outward from a ship grounding that occurred in the early 1990s. In 2014, our team established a corallimorph removal and coral transplantation experiment within the epicenter of the corallimorph outbreak, following shipwreck removal, to determine if restoration is a viable option for recovering previously dominant reef-building taxa. Monitoring of the restoration site ran from 2014-

2018 and consisted of annual surveys to assess changes in benthic community structure. By 2018, corallimorph reinvasion in experimental plots where it had been previously removed was negligible and in control plots, corallimorph cover decreased by 99%. Across the entire site, coral cover increased by 392%, turf and crustose coralline algae have dominated the remaining benthos, and coral recruits have been observed as well. Additionally, variations in growth rate and asexual propagation among coral transplant species appears to influence benthic community succession. Methods used within this study provide an effective strategy for protecting localized regions of reef most vulnerable to corallimorph invasion, namely those possessing low coral cover and in the initial stages of corallimorph invasion. Additionally, these results suggest that active reef management or restoration can drive changes benthic community succession, but only if the underlying causes of degradation have been removed.

INTRODUCTION

Coral reefs are characterized as dynamic environments that commonly experience high levels of natural disturbance including tidal emersions, hurricanes and cyclones, and disease and corallivore outbreaks. These periodic disturbances affect community succession and thus species diversity across space and time (Connell 1978). However, human impacts often produce forms of acute or chronic disturbances that can exacerbate natural disturbances, leading to synergistic effects that may diminish ecosystem biodiversity over time (Bellwood et al. 2004; Nyström et al. 2000; Smith et al. 2016). Currently, habitat degradation due to human activities is occurring at a an unprecedented rate (Steffen et al. 2015; Steffen et al. 2007; Vitousek et al. 1997) and as a result, declines in coral populations and associated ecosystem function have accelerated globally (Gardner et al. 2003; Hoegh-Guldberg et al. 2007; De'earth et al. 2012). Standard methods used to manage anthropogenic impacts on coral reefs have produced measurable benefits in some regions (e.g. Roberts et al. 2001; Cinner et al. 2006; Lester et al. 2009; Aburto-Oropeza et al. 2011), but in extreme cases, degradation can alter community composition and reef function to a point where natural recovery processes are insufficient to sustain or recover dominance of corals and other calcifying taxa (Mumby & Steneck 2008; Rinkevich 2008; Hughes et al. 2010).

In response to these “extreme” disturbances and resulting degradation, coral restoration has increased in popularity as a means of manipulating the structure of reef habitats (e.g. physical structure, community structure) with the goal of restoring or maintaining coral dominance and associated ecosystem function, goods, and services. Coral transplantation, the act attaching coral fragments onto an artificial or natural reef substrate, has become the most widely utilized technique within the field of coral restoration (Hein et al.

2017). Coral transplantation provides a unique opportunity to manipulate the composition, distribution, and abundance of coral species within a reef environment, which provides an opportunity to test how community ecological theory can be used to facilitate the recovery and maintenance of calcifier-dominated reef communities (Palmer et al. 1997). However, a majority coral transplantation endeavors have focused on the technicalities of outplanting and the initial growth and survival of focal coral colonies rather than the community-wide responses to the action itself (Hein et al. 2017; Ladd et al. 2018). Overall, scientific knowledge and critical evaluation of common management practices, including coral transplantation, are lacking within the field of coral restoration due in part to its relative infancy as a scientific discipline (Guest et al. 2011; Hein et al. 2017; Ladd et al. 2018). As coral restoration continues to increase in popularity as a tool to reduce or reverse reef degradation, there is a need to develop more rigorous scientific knowledge regarding the long-term, community-wide impacts of “restoration” based upon hypothesis driven research.

Naturally, coral reef ecosystems are composed of multiple species of corals that occur in distinct spatial distributions based on their varied life history strategies (Buss & Jackson 1979; Karlson et al. 2007; Edwards et al. 2017). The spatial patterns in which these corals, and their competitors, are distributed sets the context for growth, competition, and colonization over large spatiotemporal scales (Connell 2004; Sleeman et al. 2005; Edwards et al. 2018; Brito-Millan et al. 2019). Therefore, transplanting corals in strategic arrangements informed by species-specific life history strategy and known distributions within naturally occurring reef communities could potentially facilitate the growth and survival of corals and other “preferred” taxa within restoration sites. For instance, transplanting large, competitively dominant or fast-growing coral species in non-aggregated spatial configurations may enhance

growth, whereas competitively inferior, slower growing coral species may be more likely to persist when aggregated with conspecifics (Sleeman et al. 2005; Brito-Millán et al. 2019). Additionally, inclusion of multiple coral species can potentially enhance productivity (i.e. overyielding effect; Tilman 1999) and can lead to greater stability of coral cover over time (i.e. portfolio effect; Doak et al. 1998). However, the number of published studies that utilize multiple species of coral transplants and have taken an experimental approach to coral restoration is extremely limited (Ladd et al. 2019). Furthermore, the studies that do exist have shown variable results and overwhelmingly focus on the growth and survivorship of focal colonies rather than overall shifts in benthic community composition and function over time.

Within coral reef communities not heavily perturbed by anthropogenic activities, calcifying, reef-building organisms typically dominate the benthos while fleshy organisms, such as turf algae and non-calcifying macroalgae, occur in lower abundances (Smith et al. 2016). When environmental conditions and resource availability no longer favor dominance by reef-building taxa, fleshy organisms are capable of dominating reef substrate by outcompeting previously established individuals (Done 1992; Smith et al. 2006; Norström et al. 2009) and by reducing available substrate necessary for recruitment of previously dominant taxa (Kuffner et al. 2006). Therefore, interventions such as removing proliferations of non-calcifying organisms can produce open space needed for re-establishment corals and other key benthic functional groups. However, removal is unlikely to produce lasting shifts in community composition unless the underlying stressors that support the abundance of fleshy organisms (e.g. reduced grazer populations, poor water quality) are removed or reduced (McClanahan et al. 2002; Muthiga et al. 2002; Norström et al. 2009; Williams et al. 2001).

The coral reefs of Palmyra Atoll, an uninhabited island in the Central Pacific and part of the Pacific Remote Islands Marine National Monument, are generally considered quasi-pristine due to minimal local human impacts (Knowlton & Jackson 2008). However, certain sections of Palmyra's reefs have experienced "invasion" (here defined as the proliferation of a given taxa that has overgrown and continues to overgrow typically dominant taxa) by the corallimorph (*Rhodactis howesii*) associated with a ship grounding that occurred in 1991 (Work et al. 2008). Corallimorpharians are often characterized as opportunistic species capable of rapid replication (budding and fragmentation) and aggressive competition, particularly in degraded habitats (Chadwick-Furman et al. 2005; Kuguru et al. 2004). On Palmyra, it has been hypothesized that the ship grounding produced open space that the corallimorph could rapidly colonize and once established, it has been capable of outcompeting corals and other benthic taxa typically found on Palmyra's reefs (Carter et al. 2019). Given possibility that the shipwreck itself may have continued to facilitate corallimorph proliferation, the shipwreck was removed in 2014 (Work et al. 2008; Work et al. 2018).

In the months following shipwreck removal, our team established a corallimorph removal and multi-species coral transplantation experiment within the epicenter of the invasion to determine if coral restoration can shift impacted reefs towards dominance of corals and other reef-building taxa. Furthermore, we transplanted corals in aggregations of conspecific and heterospecifics, as well as non-aggregations to assess if and how spatial distribution may alter coral growth and community composition. We hypothesized that interspecific competition and facilitation within heterospecific aggregations will lead to the largest overall increases in coral cover. However, competitively inferior coral species will incur comparably less growth over time within heterospecific aggregations as compared the

conspecific aggregations and non-aggregated communities. Additionally, corallimorph reinvasion within experimental plots is expected to remain low, provided shipwreck and localized corallimorph removal are capable of producing shifts in resource availability that no longer favor corallimorph dominance.

In this study, we use a suite of monitoring techniques to examine how restoration impacts benthic community succession. First, we used large-area imaging techniques to track changes benthic community composition and species-specific coral cover over time. Next, we paired this imaging technique with diver surveys to quantify coral recruitment and corallimorph reinvasion. Lastly, we use calcification accretion units (CAUs) to examine early-successional benthic community structure, CaCO_3 deposition, and fleshy biomass production across time and treatment. Results herein can be used to inform management agencies on the scalability and benefit of coral restoration throughout Palmyra Atoll to mitigate continued corallimorph proliferation and reef degradation. More broadly, these results provide insight into how restoration activities may be able to drive changes in benthic community succession towards a “desired” reef condition.

METHODS

Study Location

All research took place on Palmyra Atoll, a U.S. Fish and Wildlife Service (USFWS) National Wildlife Refuge located within the Pacific Remote Islands Marine National Monument (designated in 2009). Palmyra is considered to have a ‘near-pristine’ reef community (Knowlton & Jackson, 2008) given its remote location, lack of a permanent human population, and strict regulations on human activities. However, previous occupation by the U.S. military left substantial alterations to the atoll including dredging and construction of causeways, ship channels, docks, and runways. Additionally, in 1991 a longline fishing vessel ran aground onto Palmyra’s western reef terrace, which is believed to have initiated the corallimorph invasion described in previous studies and evaluated here (Work et al. 2008; Kelly et al. 2012). In 2014, the USFWS removed the wreck to address any possible residual effects that the ship may have had on adjacent reefs (Work et al. 2018). The region of reef immediately surrounding the wreck scar—the epicenter of the corallimorph invasion—is where the experiment described below was conducted. The initial plots were selected and marked 9 months following the removal of the wreck.

Experimental Setup

Fifteen plots, each approximately 9 m², were established surrounding the wreck scar using labeled stainless steel eye bolts fixed at each corner with marine epoxy. Plots were randomly assigned to one of five treatments: (1) control, no manipulation (CON), (2) corallimorph removal (REM), (3) corallimorph removal and non-aggregated coral transplantation (RAN), (4) corallimorph removal and corals transplanted in same-species

aggregations (BYSP), and (5) corallimorph removal and corals transplanted in mixed-species aggregations (XSP) (Figure 1). When referring to groups of treatments, all treatments containing coral transplants will be referred to as ‘transplant treatments’ and all treatments not containing coral transplants will be referred to as ‘control treatments.’

In preparation for corallimorph removal, a dose-response experiment was conducted to evaluate the lowest concentrations at which three different chemicals—acetic acid, granulated chlorine, and bleach—could effectively kill the corallimorph. Granulated chlorine required the lowest concentrations needed to effectively remove corallimorph and, therefore, was used for this experiment (data not shown). All plots that received the corallimorph removal treatment were covered with 4 x 4 m tarps secured to the seafloor using sandbags, chains, and rubble and subsequently filled with 3 gal bags filled with granulated chlorine. After 48 hours, tarps were removed and any remaining corallimorph tissue was scraped off to produce a nearly 100% calcium carbonate substrate.

Pocillopora damicornis, *Montipora capitata*, and *Acropora acuminata* were chosen as our coral transplant species because of their abundance on Palmyra’s reef terrace and their differences in growth morphology and competitive ability (n=3 of each species per plot). *P. damicornis*, a hermaphroditic brooding coral (Gorospe & Karl 2013) is characterized on Palmyra as a fast-growing coral with a determinate growth pattern and short life span compensated with comparably quick regenerative capabilities through sexual reproduction (Edwards et al. 2018). *M. capitata* assumes both encrusting and plating morphologies and *A. acuminata* is a branching coral with comparably high growth rates and strong regenerative abilities through fragmentation as is consistent with other acroporid species (Highsmith 1982; Wallace 1985; Riegl & Piller 2001; Diaz-Pulido et al. 2009). In an effort to not

disproportionately harm a singular section of intact reef, coral fragments were collected from nearby reef terrace locations that had not experienced profound corallimorph invasion but were all less than 1 km from the study site. *A. acuminata* individuals approximately 25 cm in height and with at least 5 branches were fragmented from large (>2 m²) *Acropora* thickets and free-living colonies of *P. damicornis* and *M. capitata* approximately 10 cm in diameter were collected as well. Corals fragments were immediately transported to the restoration site and secured onto the bare substrate within the predesignated treatments using marine epoxy. For the RAN treatment, each plot was subdivided into 9 1 m² subplots and coral fragments were randomly assigned to one of the subplots. For the aggregation treatments (BYSP and XSP) corals were transplanted in densities of approximately 3 corals per m² and aggregations were separated by at least 2 m.

In 2015, one year following establishment of the experiment, all corallimorph polyps that had re-entered XSP, RAN, BYSP, and REM plots were removed using chisels and all coral transplants that had become detached were re-attached using marine epoxy. Coral transplants that experienced full mortality by 2015 or were no longer found within a plot were replaced as well. Given these sitewide alterations, October 2015 is considered to be the true start-date of the restoration experiment.

Benthic Imagery Collection and 3D Model Creation

Plots were studied through the collection of imagery where a diver would swim each plot in a gridded pattern approximately 1.5 m above the benthos and take approximately 1000 images (1 per sec) using a Nikon D7000 16.2 megapixel DSLR camera with an 18mm lens. Raw images were fused together to produce three-dimensional (3D) surface reconstructions of

each plot using the structure-from-motion (SfM) software Agisoft Photoscan Pro 1.3.5 (Agisoft LLC., St. Petersburg, Russia). Next, plot reconstructions were exported as dense point clouds into Viscore, a custom made software used to organize, visualize, and analyze digital representations of natural habitats (Petrovic et al. 2011; Naughton et al. 2015). To analyze reconstructions of the same plot across all sampling periods, 3D models associated with a given plot were aligned in Viscore by manually moving models in three-dimensional space until all reconstructions of a given plot were located in the same exact space with the same scale and orientation (Figure 2a). Next, each group of aligned plots were scaled to the true plot size by identifying and tagging two scale reference bars that had been placed in all plots during image collections in September 2016 and 2017, leading to four measurements of scale that were used in conjunction to increase scaling accuracy (Figure 2b). To ensure that all models had the correct depth and orientation, groups of aligned plots were oriented in batch with the use of depth measurements collected in the field from 2015-2017 (Figure 2c). Viscore uses all depth measurements associated with a given group of aligned plots and estimates correct orientation and depth which reduces impacts of erroneous measurements caused by tides and wave energy present at the time of sampling.

Virtual Point Intercept Workflow

Once all models were aligned, scaled, and oriented, Virtual Point Intercept (VPI) analysis was conducted for all 3D models. VPI is an image analysis feature within Viscore used to measure the abundance of benthic organisms within a specified region of a 3D model. In this study, VPI construction uses the same methods as described in Fox et al. 2018 with the exception that, instead of utilizing the same-sized rectangular VPI region for all 3D models,

the irregular polygonal shapes of the plots were accounted for by manually defining all regions of VPI analysis using the exact perimeter of each plot visualized within the 3D model (Figure 3a). Additionally, due to differences in shape and size of the plots and, hence the VPI regions of interest across the 3D models, the number of points generated within a region of interest could not be the exact same value for all plots. Therefore approximately 30 points per m² were generated for VPI region of interest.

Once points were distributed in a randomly stratified fashion across the desired region of the 3D model, the organism under every point was identified to the finest possible taxonomic level. This enables users to access all raw images associated with a given point within the 3D model, providing a variety images consisting of different angles and exposures with which to assign a taxonomic identification during VPI analysis, making identification more robust (Figure 3b). VPI output was converted into percent cover for all benthic functional groups and coral transplant species.

Coral Abundance

VPI analysis was used to track the change in percent cover (CPC) of each coral species within the restoration site from October 2015-September 2018. To examine the differences in coral transplant species CPC over the course of the study within the transplant treatments (XSP, BYSP, and RAN), a two-way fixed-effects analysis of variance (ANOVA)—with coral transplant species and treatment as fixed effects—was conducted. Prior to analysis, all CPC data was square root transformed to satisfy assumptions for normality and homogeneity of variances. Additionally, one-way ANOVAs were carried out for percent cover of each coral species across all timepoints and treatments (only in cases

where data met assumptions of variance and homogeneity) to compare coral cover of individuals across treatments within each time point. Post hoc comparisons for all ANOVAs were conducted using Tukey's multiple comparison test to examine interactions between factors.

Analysis of Benthic Community Composition

To measure corallimorph percent cover prior to corallimorph removal, photomosaic imagery was collected several days before chlorine treatment commenced in September 2014. All plots were partitioned into quadrats and each section was photographed using a Canon PowerShot G15 camera. Raw imagery was hand-aligned into a mosaic image using Adobe Photoshop Version 19.1.5. Next, photomosaic plot images were uploaded onto PhotoGrid 1.0 and analyzed by generating approximately 30 stratified random points per m² across the model and identifying the organism under each point. In all sampling periods post-2014, imagery was processed using the SfM workflow detailed above. Community composition data collected using the 2014 imagery is used as a baseline for all plots but is not incorporated into statistical analyses given the differences in data collection, model construction, and point count analysis between 2014 and all subsequent years. Furthermore, given that corallimorph was removed from all treatments (except for CON) once again in September 2015, all timepoints post-September 2015 are used to assess impacts of treatment type on benthic community composition.

To examine how overall benthic community composition changed in relation to treatment from 2015-2018, all organisms identified within VPC analysis were binned into functional groups consisting of corals (scleractinian coral, specifically), calcifying algae,

corallimorph (*R. howesii*, specifically), turf algae, non-calcifying algae, and nonbiological substratum. Proportional cover data of each functional group was square root transformed and Bray-Curtis dissimilarity values were produced for each time by treatment combination. The resulting dissimilarity matrix was plotted in multivariate space using non-metric multidimensional scaling (NMDS) ordination and each point associated with the same treatment was connected chronologically to produce successional trajectories. The NMDS plot displays Bray-Curtis values in two-dimensional space by preserving the ranked similarities among all values. Points that are closer together in the NMDS plot are more similar in benthic community composition as compared to points further away in ordination space. Additionally, a factorial permutation-based multivariate analysis of variance (PERMANOVA; 999 permutations) was conducted using the same Bray-Curtis dissimilarity matrix in which treatment and sampling period were both treated as fixed effects. Post hoc pairwise comparisons among factors were conducted to determine if and when treatment effects produced significant differences in community structure.

***In Situ* Ecological Surveys**

In situ surveys of coral juvenile density across all plots were conducted in 2017 and 2018. Additionally, damselfish abundance and coral colony abundance across three different size classes (>1 cm, 1-5 cm, >5 cm diameter) were surveyed in 2018. Juvenile corals are defined in this study as coral colonies ≤ 5 cm in diameter that do not possess any signs of fragmentation from a mother colony (Sandin et al. 2008). Given their propensity to fragment, *M. capitata* and *A. acuminata* colonies within the ≤ 5 cm size range observed within the

transplant treatment plots could not be differentiated between juveniles and fragments. Therefore, these individuals are left out of statistical analyses regarding juvenile density.

To determine if juvenile corals varied significantly among the treatments, juvenile density within each plot was calculated on a m² basis by dividing the total number of juveniles per plot by plot area, as determined using Viscore analytical tools. Next, juvenile density data was square root transformed to satisfy normality and homogeneity of variance and examined using a two-way fixed factor ANOVA to explore variations in juvenile density across treatments and years. Additionally, to examine the relationship between damselfish abundance and coral cover, Pearson correlation analyses were conducted on damselfish abundance per plot vs. total coral percent cover, percent cover of each coral transplant species, and abundance of *Acropora* thickets per plot in 2018.

Calcification Accretion Units

Calcification Accretion Units (CAUs) are standardized, replicable devices that measure key ecosystem processes such as coral recruitment (Rogers et al. 1984), benthic community structure, biomass production, net reef calcification (Price et al. 2012), sedimentation, and microinvertebrates (Smith et al. 2001), making them an advantageous tool to track community-wide ecological processes. In this study CAUs were used to examine changes in early-successional benthic community structure, CaCO₃ accretion and total biomass production across treatments. CAUs were assembled by stacking two PVC tiles together with a 1 cm spacer to create benthic topography including exposed surfaces, cryptic spaces, and overhangs. CAUs were mounted on stainless steel rods that were epoxied into the reef pavement. Three CAU units were installed in each plot and were collected at 12-month

intervals. In this study the first three deployment periods, 2014-2015, 2015-2016, and 2016-2017, are used for analysis.

Following collections, methods of early-successional benthic community analysis and measurement of CaCO_3 accretion rates and biomass production rates were nearly identical to methods used in Price et al. 2012. In short, all tile sides within a given CAU were photographed in seawater, rinsed with freshwater and then immediately dried before further analysis (rather than preserving them in formalin as stated in Price et al. 2012). Community composition was analyzed using the image analysis software PhotoGrid 1.0 and organisms were identified to the lowest possible taxonomic resolution. To measure biomass production, CAU tiles were dried at 65 C, weighed and then decalcified using 5% HCl to dissolve all CaCO_3 . The remaining fleshy tissue was filtered, dried, and weighed to measure the relative biomass of fleshy, CaCO_3 , and total accumulated biomass on each tile.

For statistical analysis of community composition on CAUs, taxa were binned into ecological functional groups (calcified taxa, non-calcified taxa, and nonbiological substrate) and resulting proportional cover data was square root transformed. Next, Bray-Curtis similarity measures were calculated for all communities across treatments and deployment intervals and analyzed using a PERMANOVA. Lastly, measurements of net CaCO_3 production and total biomass production were converted into production rates of $\text{grams/cm}^2/\text{year}$, log transformed to satisfy assumptions of normality and homogeneity of variance, and analyzed separately using two-way fixed-factor ANOVAs to determine if production rates varied across treatments and deployment intervals.

All multivariate analyses and ordinations within this study were conducted using Primer-e v6 and all other statistical analyses were conducted using R version 3.4.

RESULTS

Coral Abundance

Across all treatments containing coral transplants (XSP, BYSP, and RAN), coral initially covered $2.8\% \pm 0.32\%$ (mean \pm 1 SE) of the benthos in 2015 and increased to $13.5\% \pm 0.91\%$ cover by 2018. In the control treatments (CON and REM), coral accounted for $0.26\% \pm 0.26\%$ of the benthos in 2015 and increased to $1.7\% \pm 0.52\%$ of the benthos by 2018. All transplant treatments experienced significantly greater CPC over the course of the study period than the control treatments (Figure 5a; Tukey's post-hoc comparison, $p < 0.001$ for each transplant treatment vs. control treatment pairwise comparison).

***A. acuminata* Abundance**

By September 2018, *A. acuminata* reached $9.29\% \pm 0.94\%$ mean cover across the transplant treatments and accounted for 63.3% of coral cover throughout the entire experiment. Among the transplant treatments, *A. acuminata* had a higher percent cover in XSP compared to RAN in September 2017 (Tukey's; $p = 0.045$), but in all other time points, transplant treatments did not have significantly different *A. acuminata* cover (Figure 5b). Furthermore, significant *A. acuminata* CPC was not detected in any transplant treatments until September 2017 (Tukey's; $p < 0.001$ for Sept. 2015 to Sept. 2017 comparison).

***M. capitata* Abundance**

By September 2018, *M. capitata* reached $1.42\% \pm 0.20\%$ cover within the transplant treatments and accounted 9.7% of coral cover throughout the entire experiment. Unlike *A. acuminata*, *M. capitata* did not have significantly different CPC across transplant treatments in any timepoints within the study period (Figure 5c). Lastly, *M. capitata* cover increased

significantly within all transplant treatments in June 2016 (Tukey's; $p = 0.039$ for Sept. 2015 to Jun. 2016 comparison) but did not change significantly in cover for the remainder of the study period despite showing an increasing trend over time (Figure 5c).

***P. damicornis* Abundance**

By September 2018, *P. damicornis* reached $2.65\% \pm 0.31\%$ cover within the transplant treatments and accounted for 23.6% of coral cover throughout the entire experiment. Unlike *M. capitata* and *A. acuminata*, *P. damicornis* cover increased within both the transplant treatments and control treatments (Figure 5d). However, *P. damicornis* did not experience significant CPC in any of the treatments until September 2018 (Tukey's; $p < 0.001$ for Sept. 2015 to Sept. 2018 comparison), the final timepoint within the study period. In September 2018, *P. damicornis* CPC within REM was not significantly different from the three transplant treatments (Figure 5d).

Benthic Community Succession

Prior to chlorine application, corallimorph accounted for $73.79\% \pm 3.25\%$ of the benthos at the study site. Plots that were not treated with granulated chlorine (CON) experienced a 99.40% reduction in corallimorph cover from 2014 to 2018 (Figure 7a), reaching $0.52\% \pm 0.14\%$ cover across all CON plots in 2018. Corallimorph cover in plots treated with granulated chlorine remained below 5% cover throughout the entire study period (Figure 7b-d). Turf algae and calcified algae comprised the majority of the benthos in all treatments and ranged from 26.69% - 91.05% and 2.35% - 64.14% cover, respectively. Crustose coralline algae accounted for 76.45% of all calcified algae observed.

Overall benthic community composition in each time point from 2015-2018 was not significantly different across transplant treatments. However, benthic community composition within both control treatments were significantly different between one another, as well as the transplant treatments in all time points from 2015-2018 (Figure 8; Table 1).

***In Situ* Juvenile Coral and Damselfish Surveys**

Across the entire experiment, coral diversity increased from 5 species in 2014 to 12 by 2018. Although juvenile coral abundance did not experience any significant treatment effects, there was a significant increase in juvenile density across the entire site from 2017 to 2018 ($F_{1,20} = 7.641$, $p = 0.012$). *In situ* juvenile coral identification conducted in September 2017 revealed a total of 690 juveniles existing within the restoration site, 94.5% of which were *P. damicornis* (Figure 9). In 2018, juvenile abundance increased to a total of 1,260 individuals and were also dominated by *P. damicornis* (96.5% of all recruits; Figure 9).

Damselfish were observed within all plots regardless of treatment type. However, damselfish abundance had the strongest positive correlation with *A. acuminata* percent cover (Figure 10d; $r = 0.903$, $p < 0.001$), followed by overall coral percent cover (Figure 10a; $r = 0.877$, $p < 0.001$), abundance of corals >5 cm in diameter (Figure 10f; $r = 0.785$, $p < 0.001$), *M. capitata* percent cover (Figure 10e; $r = 0.732$, $p = 0.003$), and *A. acuminata* thicket abundance (Figure 10c; $r = 0.727$).

CAU Community Composition and Production Rates

Overall community composition measured on CAU tiles differed significantly across deployment intervals and treatments, but the interaction between both factors was insignificant (Table 2a). In the 2016-2017 deployment interval, CAU community composition reached its highest sitewide percent cover of calcifying taxa ($58.24\% \pm 2.25\%$) and, concurrently, the lowest sitewide non-calcifying organism percent cover over the course of the study period (Figure 11a; $33.27\% \pm 2.14\%$). In contrast, the 2015-2016 deployment interval experienced the lowest calcifier percent cover ($36.22\% \pm 0.99\%$) and the highest percent cover of nonbiological substrates ($15.62\% \pm 1.13\%$), which predominately consisted of bare CaCO_3 (Figure 11a).

CaCO_3 accretion rates, non-calcified biomass production rates, and total biomass production rates did not differ across treatments, however there were significant differences between deployment intervals (Figure 11b-c). Rates of CaCO_3 accretion and total biomass production were significantly lower in 2015-2016 in comparison to the two other deployment intervals. In 2016-2017, accretion rate, fleshy biomass production rate, total biomass production rate increased to levels significantly greater than both previous deployment periods (Figure 11b-c). Overall, there was a 29% increase in CaCO_3 accretion rate, 59% increase in fleshy biomass production rate, and a 33% increase in total biomass production rate over the course of the study period (2014-2018).

DISCUSSION

Coral Abundance

In this study, we report community-wide shifts in benthic community structure that appear to be strongly influenced by treatment effects (corallimorph removal and coral transplantation). The experiment was initially designed to assess if and how the spatial arrangement of coral transplants would affect growth and survivorship of three different species of common corals. Within the timescale of this experiment (4 years), we did not observe any treatment effects on coral abundance and growth. However, we observed differences in life history strategy among coral transplant species that have helped shape coral community structure throughout the entire study site. Interestingly, coral cover within transplant treatments did not increase significantly until September 2017, two years post-transplantation, highlighting the impact that temporal scale of monitoring has on the perceived outcome of the restoration efforts.

In the first two years of this experiment, CPC of all corals across the entire experiment was modest to nonexistent, increasing from $1.79\% \pm 0.40\%$ cover in 2015 to $2.54\% \pm 0.53\%$ cover in 2016. Previous studies have reported reduced coral growth rates following transplant establishment which they attribute to a “stress period” where transplants acclimate to their new environment (Lirman et al. 2010; Forrester et al. 2012; Forrester et al. 2014). In this study, it was likely a mixture of acclimatization and a warm water and subsequent bleaching event (occurred throughout Palmyra Atoll’s coral reefs from June–September 2015, described here (Fox et al. 2019)), that reduced coral fitness (Fine & Loya 2003) and caused reduced CPC at the beginning of the study period. However, from September 2016–September 2018, a

different trend emerges in which coral cover increases dramatically within transplant treatments, particularly among *A. acuminata*.

Branching acroporids such as *A. acuminata* are considered a fast-growing taxa that can outcompete adjacent corals via comparably rapid skeletal extension, reducing light and substrate availability (Baird & Hughes 2000). In 2017, *A. acuminata* cover was significantly higher in XSP than the RAN treatment, indicating that synergistic impacts of aggregation and mixed-species interactions may have facilitated *A. acuminata* growth, but this trend was not evident in any other time points. Previous studies have documented enhanced growth and survivorship of corals within heterospecific aggregations that appears to be a result of complementarity effects among species, but similar to this study, the ability of these interactions to alter coral growth can change with community age (Dizon & Yap 2005; Clements & Hay 2019). It is possible that XSP did not enhance *A. acuminata* growth prior to 2017 because, given that corals were transplanted at densities of 3 corals per m², there was ample space for coral colonies to grow with limited coral-coral competition, thus limiting intraspecific interactions which may enhance *A. acuminata* growth. Additionally, in 2018, damselfish abundance was highly correlated with *A. acuminata* percent cover and it was common to see larger *A. acuminata* thickets with multiple damselfish territories. Although *A. acuminata* cover continued to increase from 2017-2018, the influx of damselfish and resulting algal territories likely reduced live tissue on *A. acuminata* colonies (Myrberg et al. 1967; Ceccarelli et al. 2005; Vermeij et al. 2015), causing decreased CPC from 2017–2018. However, regardless of these potential limiting factors, *A. acuminata* provided the largest contribution to coral cover and topographic complexity at the study site through the production of dense coral thickets. Therefore, fast-growing, branching coral species such as *A.*

acuminata appear to be beneficial for coral restoration efforts aimed at increasing coral cover and topographic complexity in relatively short time frames.

In contrast to *A. acuminata*, *M. capitata* incurred the smallest increase in coral cover across transplant treatments. On Palmyra Atoll, *M. capitata* appears to have generally slower growth rates (J.E.S., personal communication) and greater thermal sensitivity compared to other common corals on Palmyra (Fox et al. 2019). However, *M. capitata* was the only coral species to increase significantly in cover directly following the 2015 bleaching event, which may be due to increased heterotrophic feeding during bleaching and recovery (Grottoli et al. 2006). In the years following the bleaching event (2016-2018), *M. capitata* did not show any significant increases in cover across transplant treatments. In fact, *M. capitata* was the only coral species to experience a net decrease in any of the plots, which occurred in one of the XSP plots and is likely the result of shading and encroachment by *A. acuminata* thickets. Although the competitive asymmetry between *A. acuminata* and *M. capitata* did not produce widespread reductions in *M. capitata* cover within all XSP plots, continued growth of *A. acuminata* thickets will likely increase competitive interactions between these two corals, shifting coral community composition accordingly (Connell et al. 2004). Additionally, it is important to note that *M. capitata* colonies experienced disproportionately greater parrotfish predation throughout the study site as evidenced by bite scars on the skeletons and observations of parrotfish predation by divers (J.E.S., personal communication). This may have produced clustered spatial distributions of *M. capitata* regardless of initial spatial distribution of transplants. As parrotfish feed on *M. capitata* colonies, they decrease colony size while simultaneously dispersing *M. capitata* fragments in the process (Mccauley et al. 2014). Although it is difficult to determine if predation has directly impacted *M. capitata*

cover, it appears to have influenced its ability to propagate throughout the study site, which is likely to impact the health and ecology of these corals in the future (Mccauley et al. 2014).

Unlike *A. acuminata* and *M. capitata*, *P. damicornis* experienced increases in cover not only within the transplant treatments, but within the control treatments as well. *P. damicornis* is a hermaphroditic brooder that releases larvae throughout the year (Tanner 1996). These larvae typically possess higher survival rates in both the water column and post-larval settlement, making them particularly adept at colonizing available substrate (Connell et al. 2004; Darling et al. 2012). Given the large spatial distribution of *P. damicornis* colonies throughout the restoration site, it appears that *P. damicornis* abundance is more closely related to larval recruitment and subsequent growth rather than propagation via skeletal extension and fragmentation of original transplants. Furthermore, as *A. acuminata* continues to increase in cover within the transplant treatments, continued *P. damicornis* colonization and subsequent growth in regions of reef devoid of *A. acuminata* (i.e. control treatments), may compensate for potential decreases in *P. damicornis* cover caused by shading and encroachment of *A. acuminata* within the transplant treatments. The ability of *P. damicornis* to evade coral competition via larval recruitment is likely to impact coral community structure and may help maintain greater coral diversity at the study site, especially if *A. acuminata* continues to usurp available substrate within transplant treatments (Connell 1978; Connell et al. 2004). Therefore, although *P. damicornis* may not produce the same structural complexity that *A. acuminata* is capable of producing, it appears to be a beneficial coral transplant species for restoration practitioners looking to increase coral colony abundance and coral larvae recruitment. However, the ability of *P. damicornis* to widely disperse and produce new colonies was not widely detectable at our restoration site until September 2018, 3 years post

transplantation, highlighting the importance of monitoring restoration efforts on timescales that are consistent with the growth and recruitment rates of key ecosystem engineers (Smith et al. 2010; Hein et al. 2017).

***In Situ* Juvenile Coral Surveys**

Except for the CON treatment in 2017, juvenile coral density across the entire experiment in 2017 and 2018 is similar to previous measurements of juvenile abundance at Palmyra Atoll (Sandin et al. 2008; Pedersen et al. 2019), but only if *P. damicornis* juveniles are included within this measurement. Coral recruits consisting of species other than the three transplanted coral species were also present throughout the restoration site, but in both survey periods, they did not reach densities greater than 2 juveniles per m², indicating that, although a peripheral larval pool exists, there is a possibility that recruitment at this site may be delayed without the addition of *P. damicornis* transplants. However, *P. damicornis* juveniles had been observed in the same region as our experiment in years previous to experiment establishment (Work et al. 2018). Therefore, it is plausible that recruitment at the restoration site would be comparable to other regions of Palmyra's reef regardless of whether coral transplantation had occurred.

Benthic Community Succession

Settlement and growth of coral recruits and continued growth of established corals is largely dependent upon substrate type and surrounding benthic organisms (Hughes et al. 2007; Smith et al. 2010). At the restoration site, open space produced by corallimorph removal, as well as corallimorph recession within CON treatments, was colonized

predominately by tightly cropped turf algae and CCA, indicating top-down regulation by herbivores (Smith et al. 2010). Although herbivore metrics were not recorded within this study, Davis et al. (2018) monitored changes in fish population biomass and composition surrounding the longliner wreck site (< 1 ha. from our study site) from 2014-2017 and found that herbivorous fish biomass increased as corallimorph cover decreased over time (Davis et al. 2018). Grazers such as herbivorous reef fishes reduce the biomass of alga that compete with corals and keep turf algae tightly cropped to the substrate, which indirectly promotes the abundance of CCA (Smith et al. 2010; Adam et al. 2011; Fox et al. 2019). CCA is a calcifying group of algae that is known to enhance coral larval settlement (Morse et al. 1988; Heyward & Negri 1999; Harrington, 2004; Tebben et al., 2015). Therefore, increases in coral cover and juvenile density throughout the study site are likely facilitated by reductions in corallimorph abundance and subsequent increases in tightly cropped turf algae and CCA.

Disturbance events and resource pulses allow species to overcome resource-dependent recruitment and growth limitations and can lead to turnovers in dominant taxa (Tilman 2004). At our study site, shipwreck removal paired with localized corallimorph removal appears to have produced a secondary disturbance event capable of shifting environmental conditions to a state that no longer facilitates corallimorph dominance (as described in Carter et al. 2019). As corallimorph decreased in CON treatment plots and reinvasion rates remained low to nonexistent in all other treatment plots, the benthos became colonized by taxa typically dominant on Palmyra's non-degraded reefs, including turf algae, CCA, and corals. However, the relative abundance of these taxa over time was not identical across all treatments. For instance, benthic successional trajectories between both control treatments were significantly different from one another and was likely caused by delays in recruitment of corals and CCA

within the CON treatment due to preemption of space by corallimorph in the beginning of the study period. Additionally, coral transplantation disproportionately increased coral cover within the transplant treatments compared to the control treatments. Although spatial distribution of transplants did not appear to significantly alter benthic community composition among transplant treatments, as coral transplants continue to grow, competitive interactions (particularly among aggregated transplants) are likely to increase and may lead to divergent benthic successional trajectories among the transplant treatments (Connell et al. 2004). Differences in benthic community succession across treatments are likely to play an important role in the dynamics and function of this reef site well into the future (Tilman 1999).

CAU Community Composition and Production Rates

Lastly, this study documents the first use of CAUs as a tool to monitor key ecosystem processes in relation to coral reef restoration. Early-successional benthic community composition, reef accretion rate, non-calcified biomass production rate, and total biomass production rate did not vary significantly between treatments, but each metric changed over time and appear to be correlated with the 2015 ENSO-induced Palmyra bleaching event. For instance, the 2015-2016 deployment interval had the lowest accretion and total biomass production rates, lowest calcifying taxa abundance, and the largest abundance of nonbiological substrate (bare CaCO₃ specifically) compared to all other deployment intervals. Past studies have associated elevated seawater temperatures with decreased calcification rates of benthic reef organisms (Coles and Jokiel 1978; Jokiel and Coles 1990), particularly CCA (Anthony et al. 2008; Martin & Gattuso 2009; Diaz-Pulido et al. 2012), a common organism found on CAUs as well as the surrounding benthos. It is highly probable that the warm water

event reduced the productivity of many benthic organisms throughout Palmyra's reefs, leading to reduced calcification and recruitment as detected by the CAUs. Furthermore, exposure to temperatures above the thermal optima can result in declines in calcification and growth rates in corals (Pratchett et al. 2015). Therefore, reductions in accretion rate on CAUs may be reflective of reduced calcification in nearby corals, potentially explaining the minimal-to-nonexistent coral CPC from 2015-2016 at the study site.

In the deployment interval following the warm water event, calcifying taxa percent cover increased to levels similar to the pre-ENSO deployment period. Additionally, accretion rate and non-calcified biomass production rate from 2016-2017 increased to levels greater than the pre-ENSO deployment period. Once again, these increases reflect similar changes on the benthos, where coral CPC significantly increased throughout all transplant treatments and calcified algae showed an increasing trend in abundance across the entire site in September 2017. Therefore, CAUs can potentially serve as a tool for tracking calcifier growth and reef-building capacity, although more research should be conducted to further establish the associations between CAU calcification metrics and measurements of growth and accretion in corals and other common reef-builders. Regardless, sitewide increases in accretion rate, CAU calcifier abundance, and coral percent cover approximately one year following a warm water event highlights the capacity of this location to recover immediately following an acute disturbance event, a characteristic attribute of reef resiliency (Hughes et al. 2010; Pratchett et al. 2015; Fox et al. 2019).

CONCLUSION

As coral restoration continues to increase in popularity as a tool to manage coral reef degradation, it is of utmost importance to consider how ecological processes such as community succession and competition ultimately affect the structure of the entire reef community, and thus, the effectiveness of restoration efforts (Palmer et al. 1997). In this study, we report shifts in benthic community structure that have appeared as a result of the presence or absence of invasive species removal and multi-species coral transplantation. Palmyra Atoll is a unique site for restoration given its remote location and magnitude of environmental protection; therefore, observations from this study may not be completely replicable in other locations. However, methods used within this study can be tailored to meet the specific needs of a given reef. For instance, removal of over-proliferating non-calcifying taxa may be particularly beneficial on reefs where natural consumers exist but are currently unable to provide sufficient grazing pressure to control continued proliferation (Williams et al. 2001; Muthiga et al. 2002). Additionally, utilizing multiple coral species with different life history strategies could provide a portfolio effect as seen in this study; *A. acuminata* incurred the largest increases in cover, but only in localized regions of reef, *M. capitata* experienced the least growth, but was the only species capable of increasing in cover during a bleaching event, and *P. damicornis* was able to quickly colonize larger regions of reef through sexual reproduction, but does not provide the same structural complexity of *A. acuminata*. Species trade-offs as seen in this study may lead to greater temporal stability of coral communities, particularly in regions prone to disturbance (Tilman 1999; Yachi & Loreau 1999; Connell et al., 2004; Dizon & Yap, 2005). However, changes in benthic community succession associated with multi-species coral transplantation will be strongly influenced by the choice

of transplant species and their interactions with the surrounding environment. Therefore, restoration practices that incorporate a holistic approach tailored to the local ecology and associated disturbance regime are more likely to achieve their desired restoration outcome.

FIGURES AND TABLES

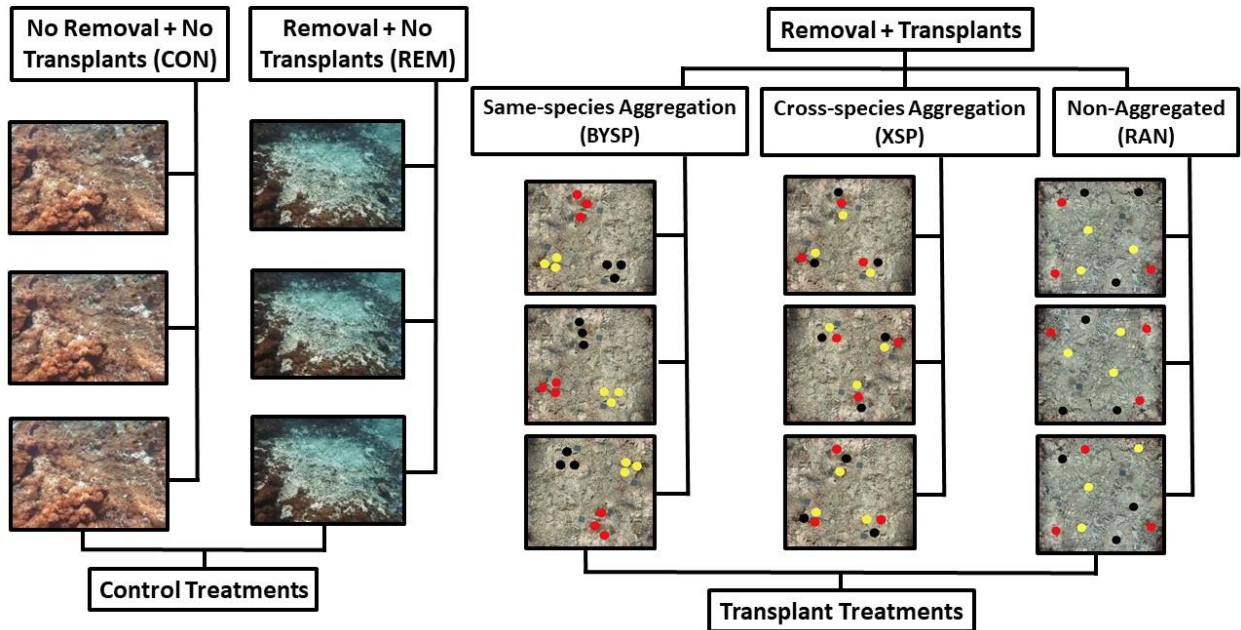


Figure 1. Schematic of experimental design. Each box represents an individual plot within a given treatment. Dots within the transplant treatment plots indicate the location and species of each coral transplant with different colors representing a different coral transplant species.

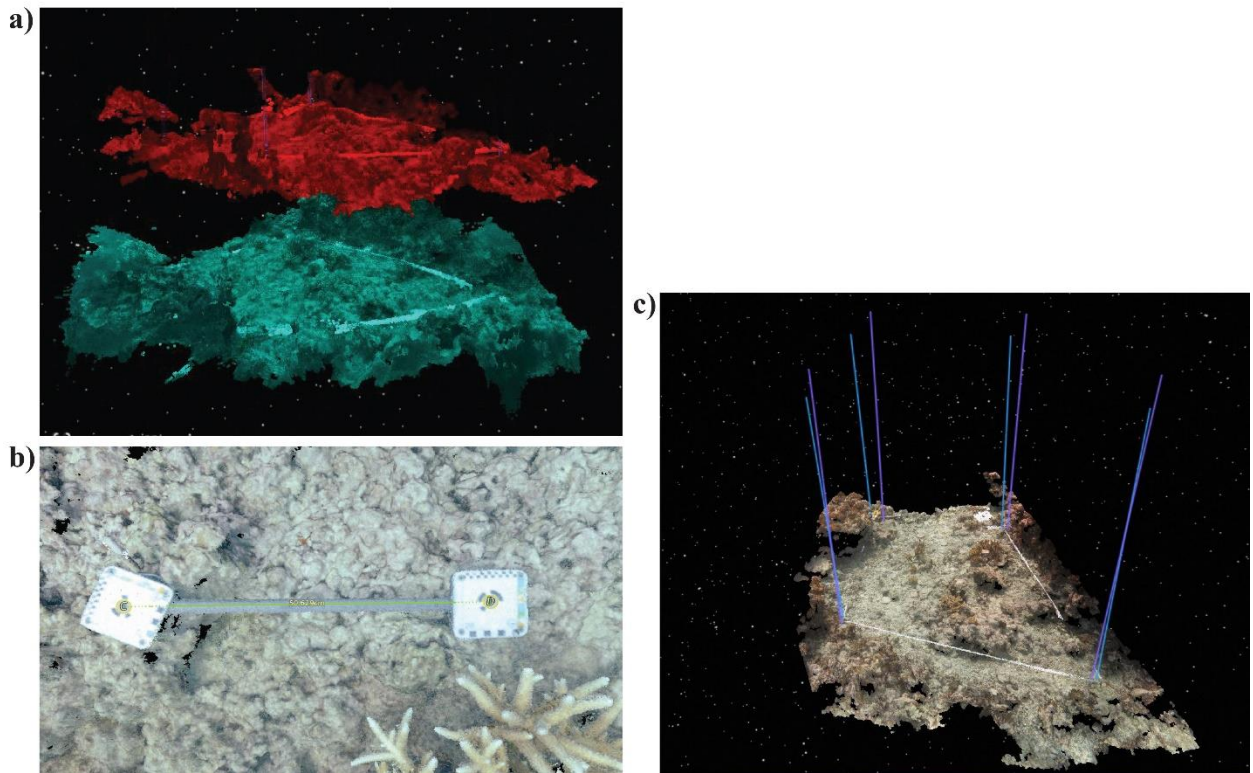


Figure 2. Viscore model calibration including a) aligning 3D models containing the same plot, but from different time points (models are shaded in opposing colors to enhance model differences during alignment), b) scaling aligned models using pre-measured calibration sticks (exact distance between targets is estimated at 50 cm and averaged between both timepoints in 2017 and 2018) and c) orienting models together by comparing depths of the same plot within different years (blue lines indicate the measurements from this individual plot whereas the purple lines represent the approximated true depths and orientation of this plot utilizing data from multiple aligned models).

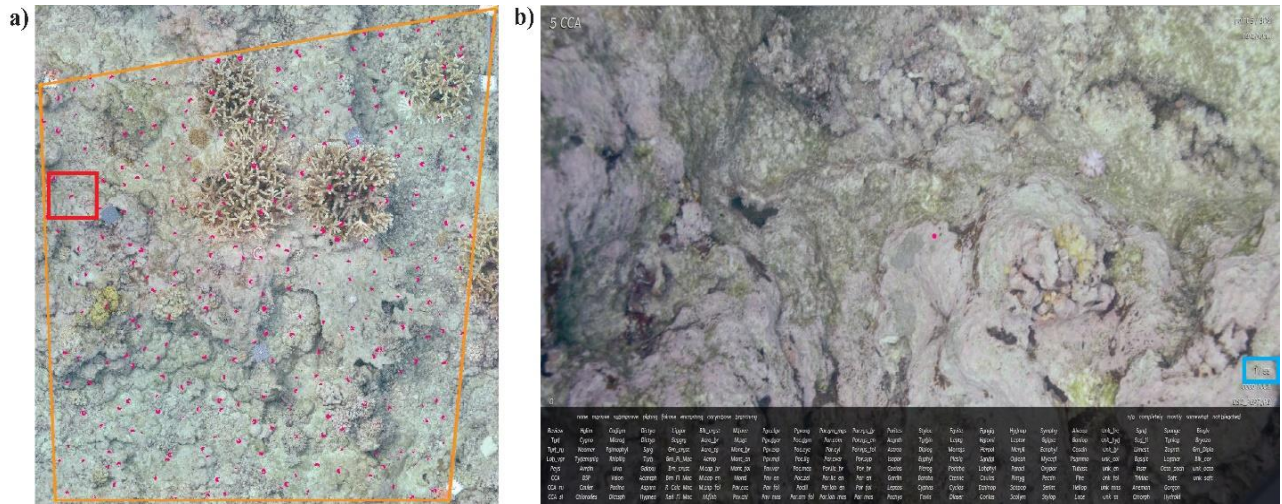


Figure 3. VPI workflow including a) defining the VPI study region (region outlined by the orange box) and generating randomly stratified points throughout the defined region (pink points) and b) utilizing a web-based point identification interface that displays all high-resolution images associated with a specific point within the study region (location within study region is outlined by the red box). In this example, there are 55 raw images associated with this given point (as indicated by the value within the blue box).

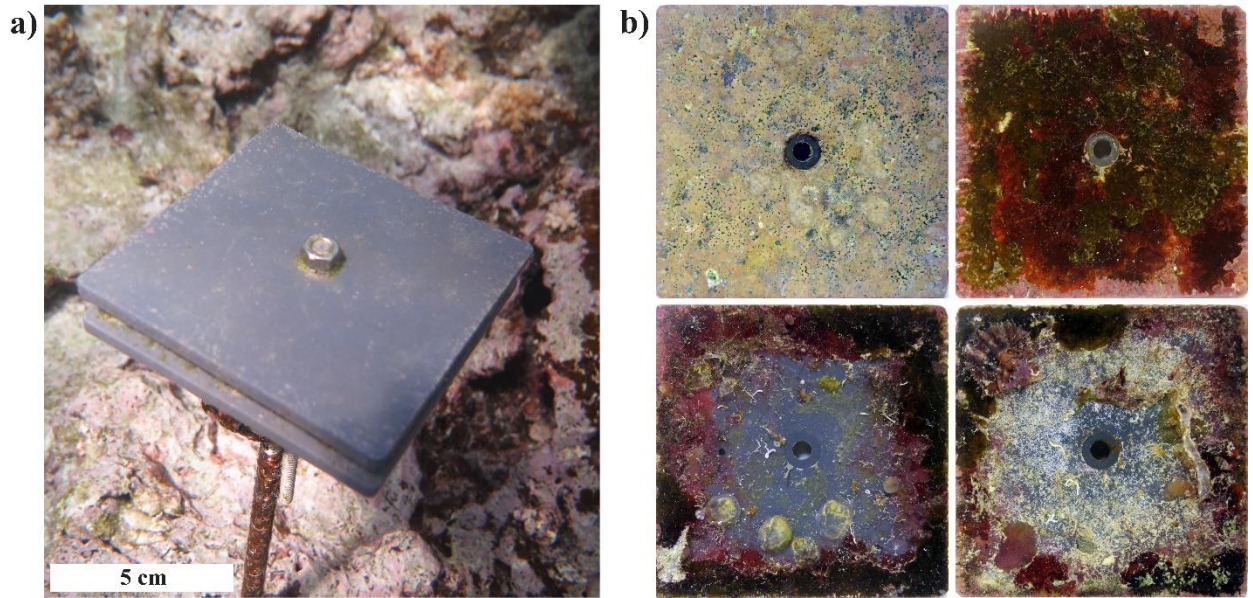


Figure 4. CAU workflow including a) deployment at the study site and b) representative photographs of exposed (top) and internal (bottom) tile sides after a year-long deployment at the restoration site.

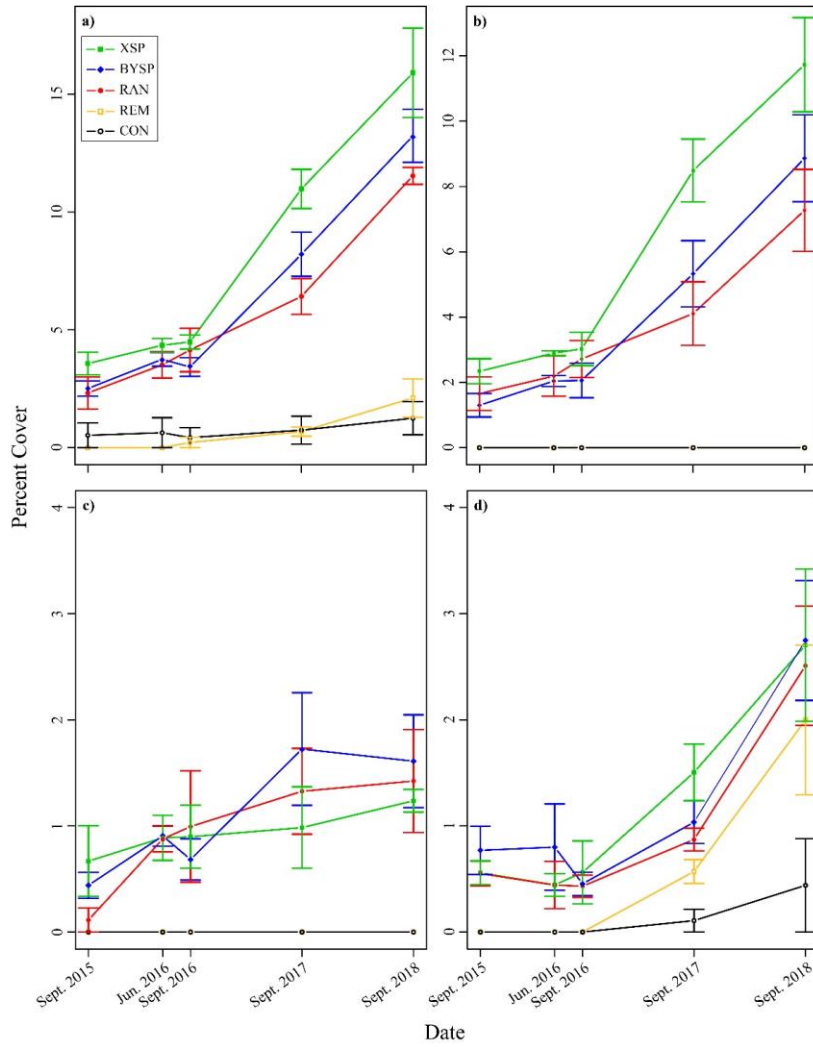


Figure 5. Percent cover (mean \pm 1 SE) of a) all coral, b) *A. acuminata*, c) *M. capitata*, and d) *P. damicornis* within each treatment from 2015-2018. Y-axes are fitted to each individual graph.

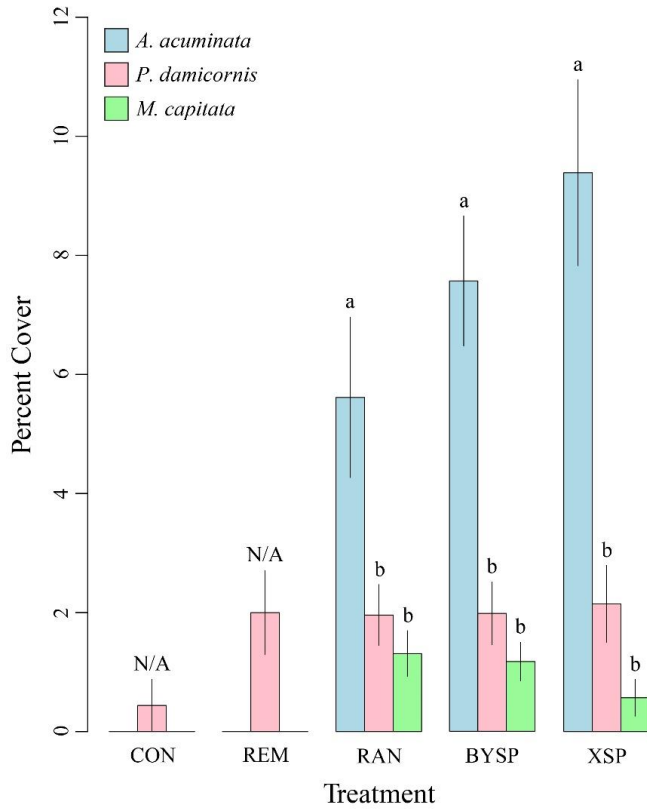


Figure 6. Change in percent cover (CPC) of each coral transplant species across all treatments from 2015-2018. Letters represent significant differences across species and treatments derived from post-hoc Tukey's multiple comparison test. Control treatments (CON and REM) are not included in statistical analysis due to non-parametric parameters. Data are reported as means \pm 1 SE.

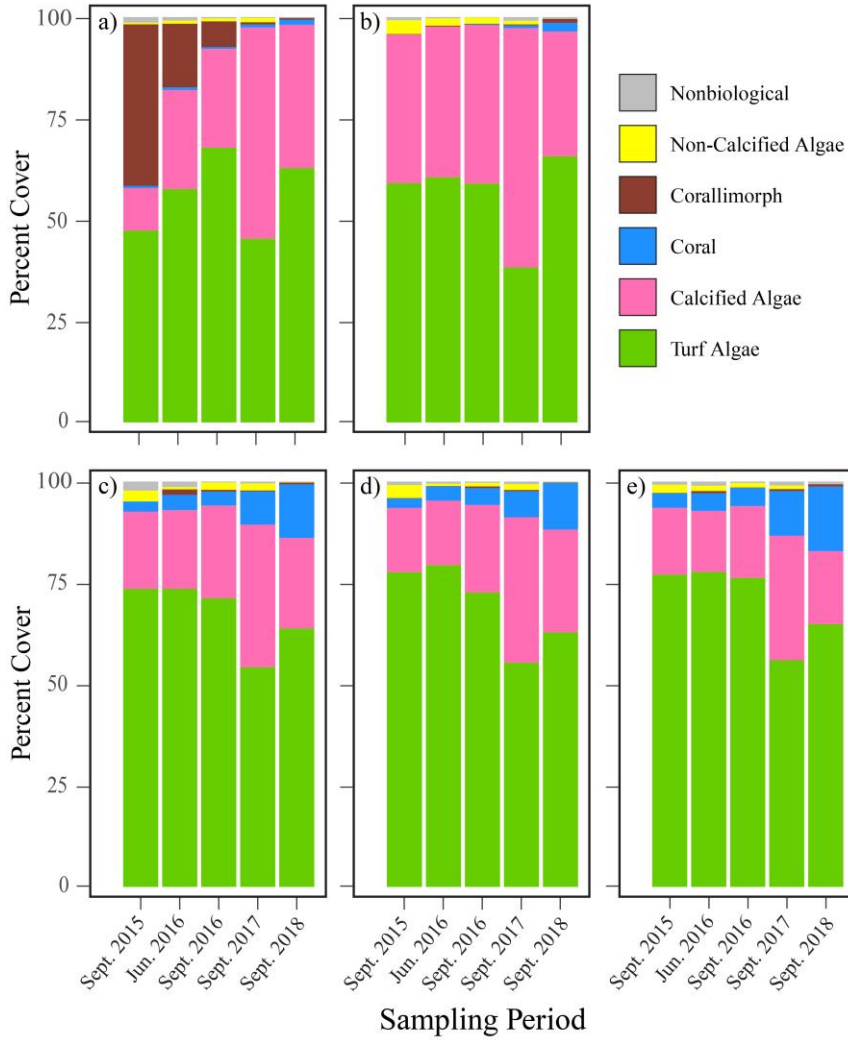


Figure 7. Benthic community composition of a) no removal + no transplants (CON) b) removal + no transplants (REM), c) removal + non-aggregated transplants (RAN), d) removal + transplants aggregated by species (BYSP), and e) removal + transplants aggregated across species (XSP) treatments from September 2015 – September 2018. Data shown are the mean values for each functional group.

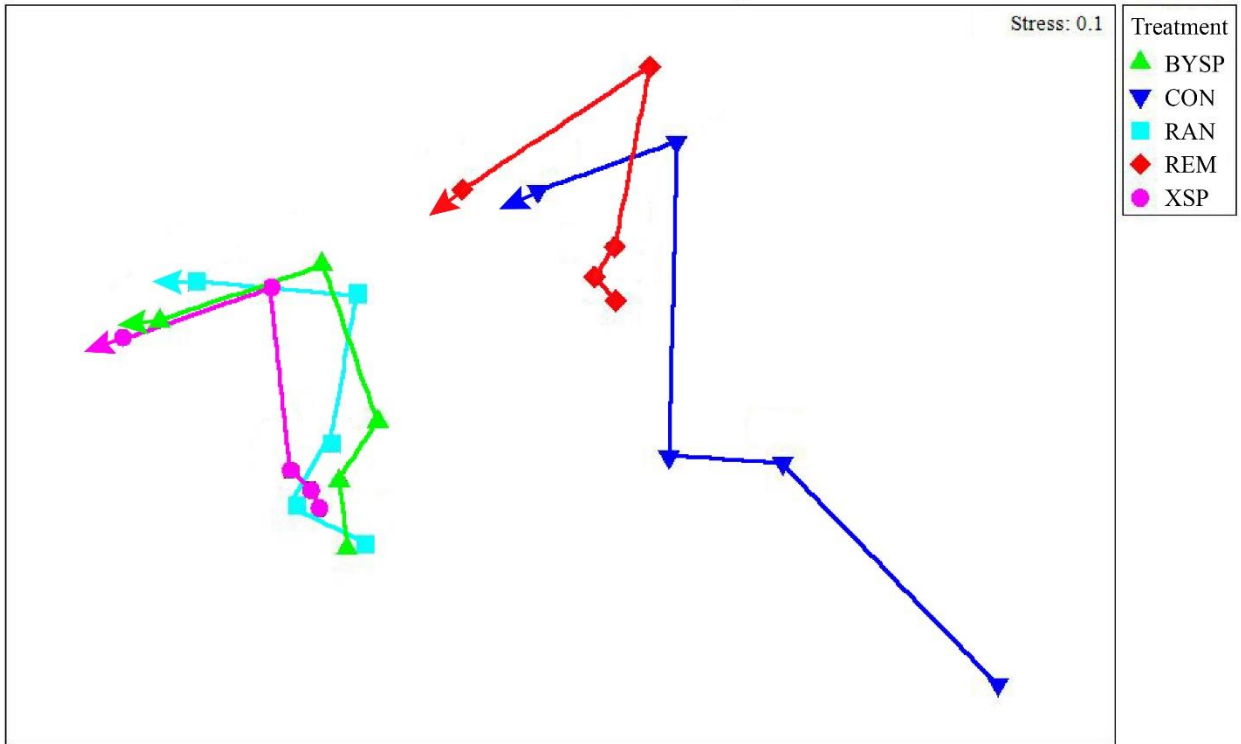


Figure 8. NMDS plot of the benthic successional trajectory of each treatment from 2015-2018. Points represent Bray-Curtis dissimilarity values for each treatment-by-time point combination and the distances between each data point indicates the magnitude of similarity in benthic community composition. For identification purposes, the final point of each successional trajectory (i.e. September 2018) is labeled with an arrow.

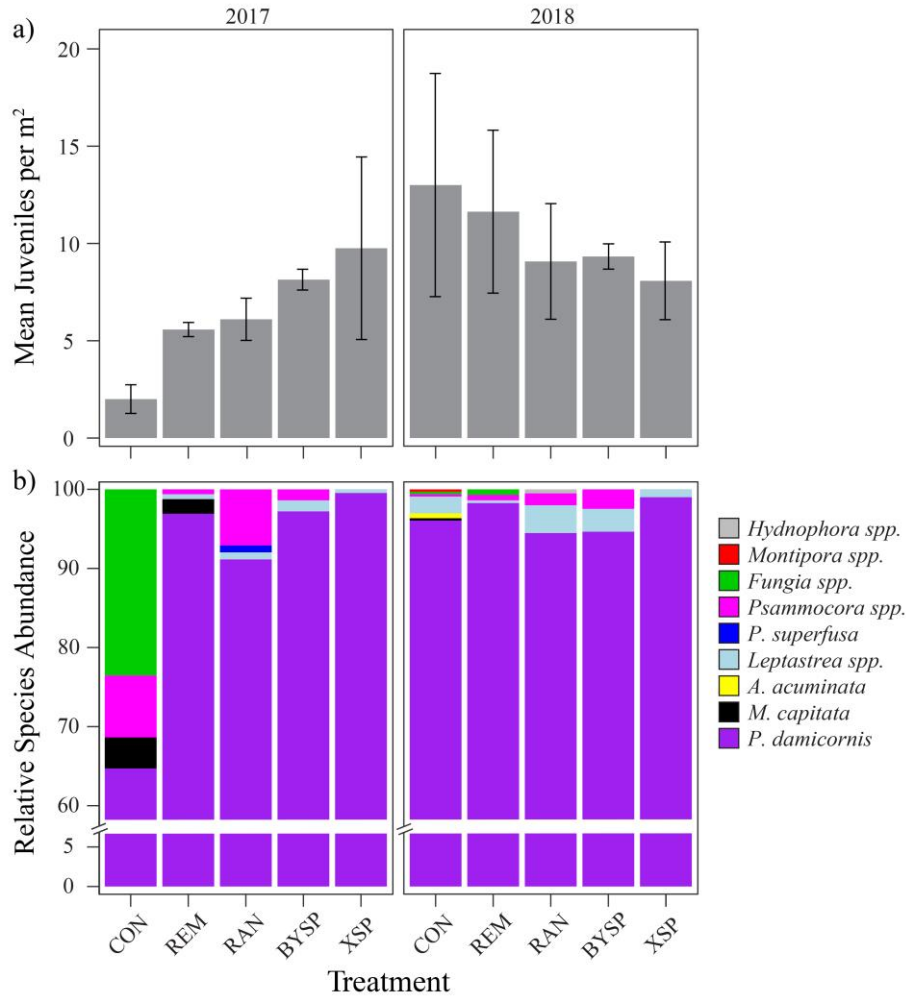


Figure 9. Mean density of juvenile corals per m² and b) relative abundance of each coral species (or genus depending on highest taxonomic resolution possible) identified at the restoration site within all treatments in September 2017 and September 2018. Error bars indicate ± 1 SE.

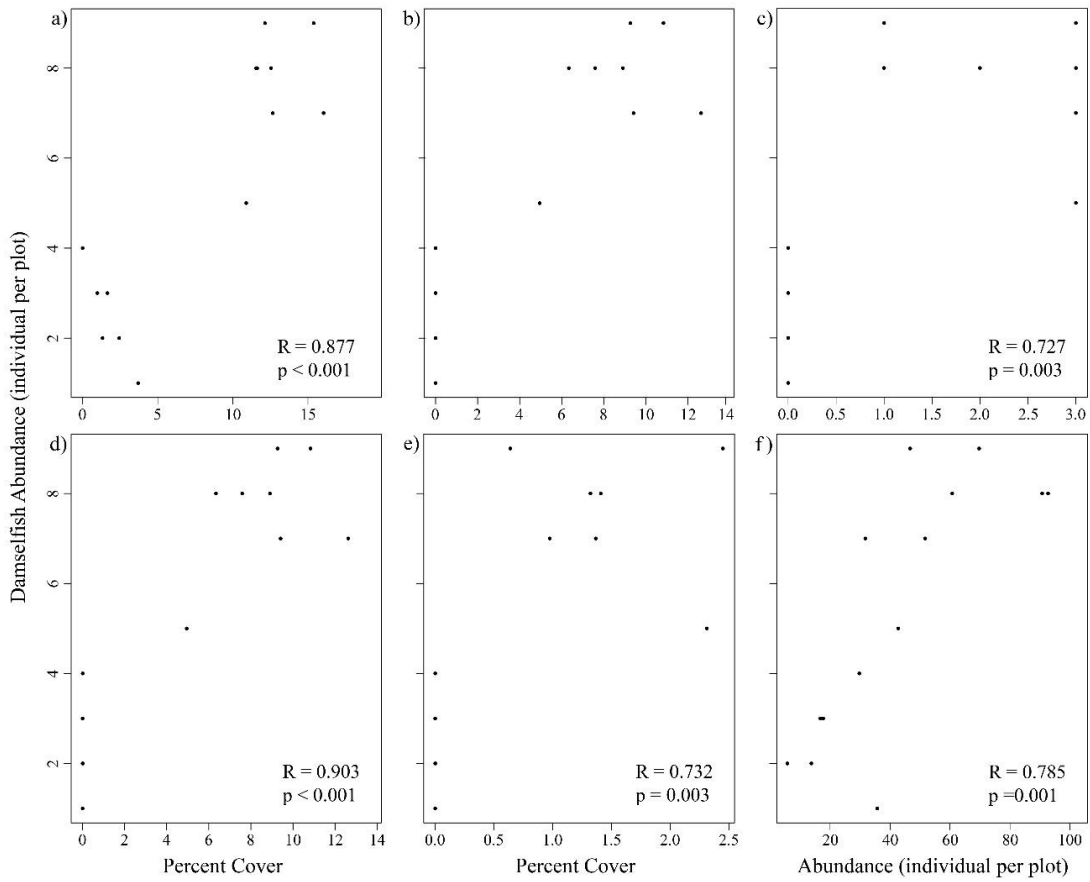


Figure 10. Relationship between damselfish abundance and a) coral percent cover, b) *P. damicornis* percent cover, c) *A. acuminata* thickets per plot, d) *A. acuminata* percent cover, e) *M. capitata* percent cover, and f) corals >5 cm in diameter recorded in September 2018.

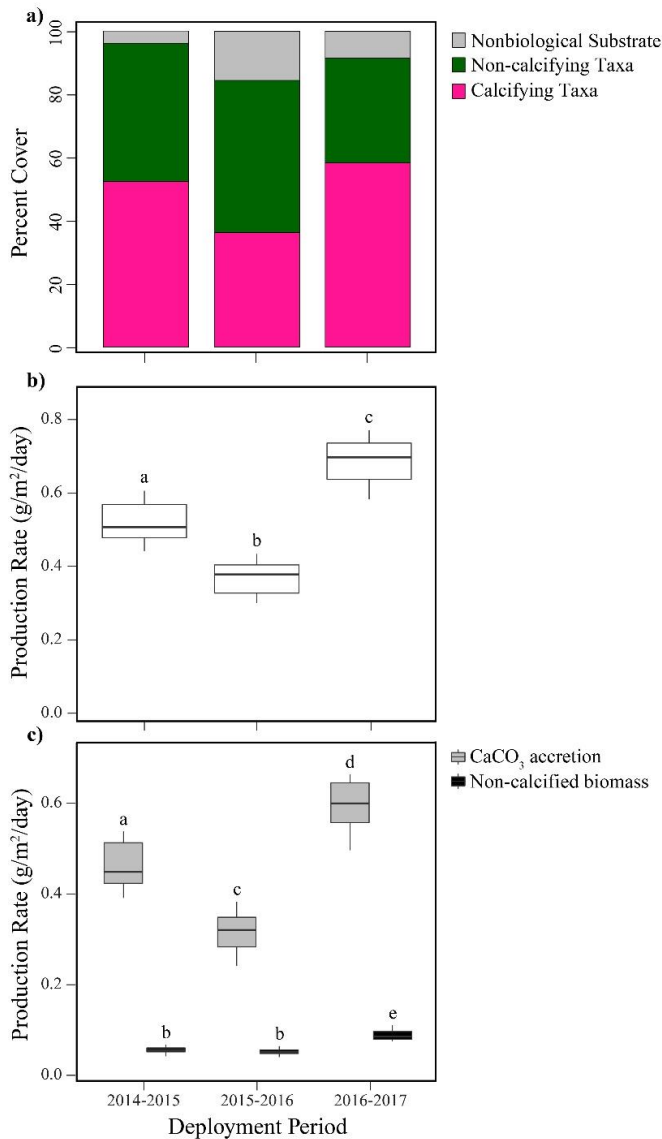


Figure 11. Results from CAU devices including a) percent composition of each ecological functional group (data shown are the mean values for each functional group) and box and whisker plots of b) sitewide total biomass production rates and c) sitewide accretion rate and fleshy biomass production rate across deployment periods. Letters indicate significant differences in production rates (Tukey's post-hoc comparison, $p < 0.001$ for all significance pairwise comparisons) between deployment periods as interpreted from one-way ANOVAs. Treatment effects were not found for community composition, total or fleshy biomass production rates or reef accretion rates and are, therefore, not included within this figure.

Table 1. Results of a PERMANOVA testing differences in overall benthic community composition across treatments from 2015-2018.

a. PERMANOVA results of benthic community composition

Source	df	SS	MS	Pseudo-F	P-value
Year	4	5087.400	1271.900	11.599	0.001*
Treatment	4	9416.000	2354.000	21.469	0.001*
Year x Treatment	16	2463.700	153.980	1.404	0.102
Residuals	50	5482.400	109.650		
Total	74	22450.000			

b. PERMANOVA pairwise comparisons of benthic community composition (only groups with $p < 0.05$ displayed)

Treatments	t	P-value
REM vs. RAN	5.239	0.001
REM vs. BYSP	4.931	0.001
REM vs. XSP	6.637	0.001
REM vs. CON	3.500	0.001
RAN vs. CON	5.749	0.001
BYSP vs. CON	5.324	0.001
XSP vs. CON	6.608	0.001
Years		
Sept. 2015 vs. Sept. 2016	1.809	0.039
Sept. 2015 vs. Sept. 2017	4.326	0.001
Sept. 2015 vs. Sept. 2018	4.804	0.001
Jun. 2016 vs. Sept. 2017	3.897	0.001
Jun. 2016 vs. Sept. 2018	3.758	0.001
Sept. 2016 vs. Sept. 2017	3.563	0.001
Sept. 2016 vs. Sept. 2018	4.021	0.001
Sept. 2017 vs. Sept 2018	4.340	0.001

Table 2. Results of a PERMANOVA testing differences in CAU community composition across treatments and deployment intervals.

c. PERMANOVA results

Source	df	SS	MS	Pseudo-F	P-value
Deployment	2	1461.000	730.500	64.800	0.001*
Treatment	4	151.320	37.829	3.356	0.004*
Deployment x Treatment	8	163.280	20.041	1.811	0.057
Residuals	30	338.190	11.273		
Total	44	2113.800			

d. PERMANOVA results of pairwise comparisons among treatments and among deployment intervals (only groups with $p < 0.05$ displayed).

Treatments	t	P-value
CON vs. BYSP	1.937	0.043
REM vs. BYSP	1.937	0.044
CON vs. RAN	2.978	0.005
RAN vs. XSP	2.391	0.012
Years		
2014-2015 vs. 2015-2016	10.475	0.001
2014-2015 vs. 2016-2017	4.945	0.001
2015-2016 vs. 2016-2017	8.998	0.001

APPENDIX

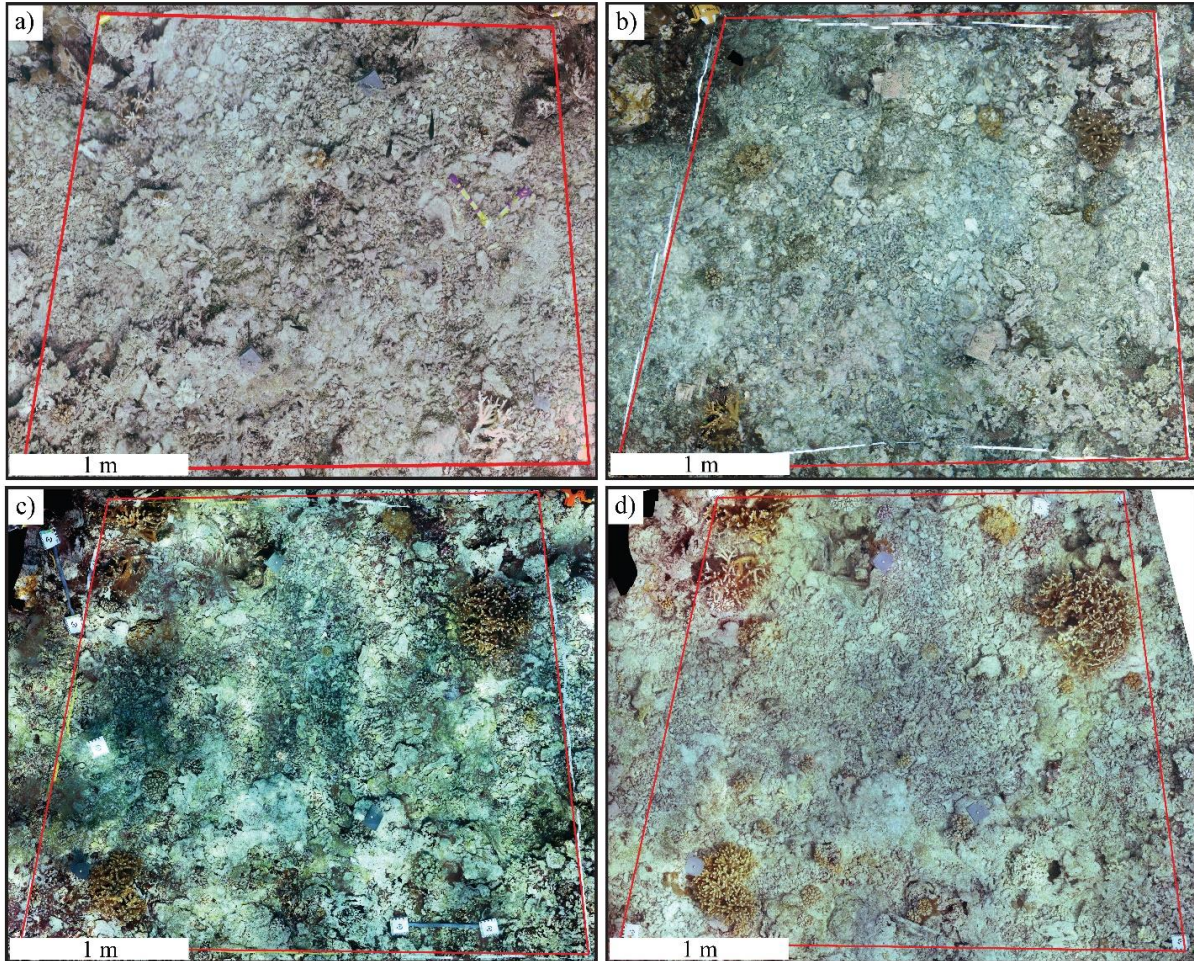


Figure 12. Orthophotos (define orthophotos) of a representative removal + non-aggregated transplants (RAN) treatment plot across time in September 2015 (top left), June 2016 (top right), September 2017 (bottom left), and September 2018 (bottom right).

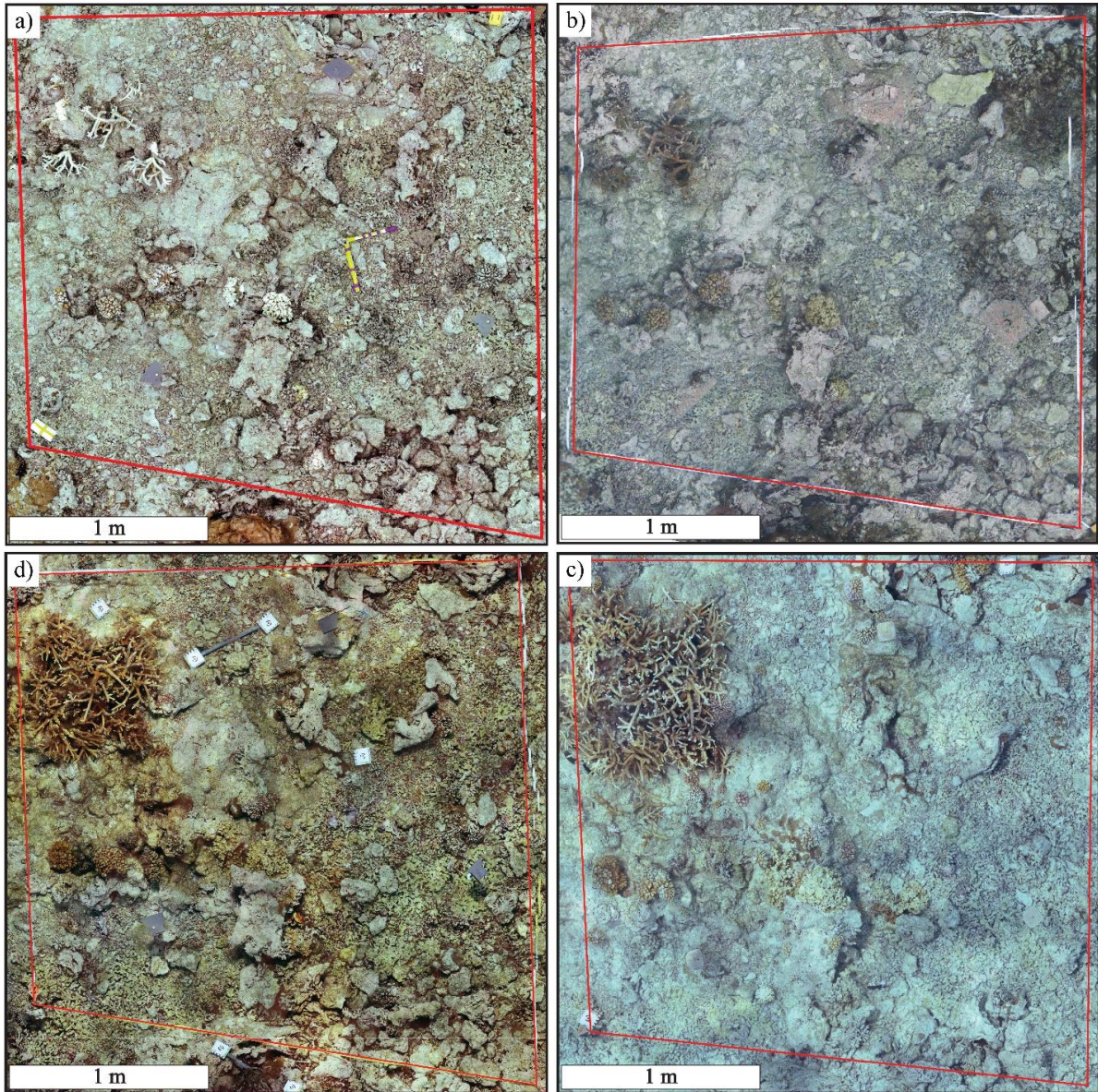


Figure 13. Orthophotos of a representative removal + transplants aggregated by species (BYSP) treatment plot across time in September 2015 (top left), June 2016 (top right), September 2017 (bottom left), and September 2018 (bottom right).

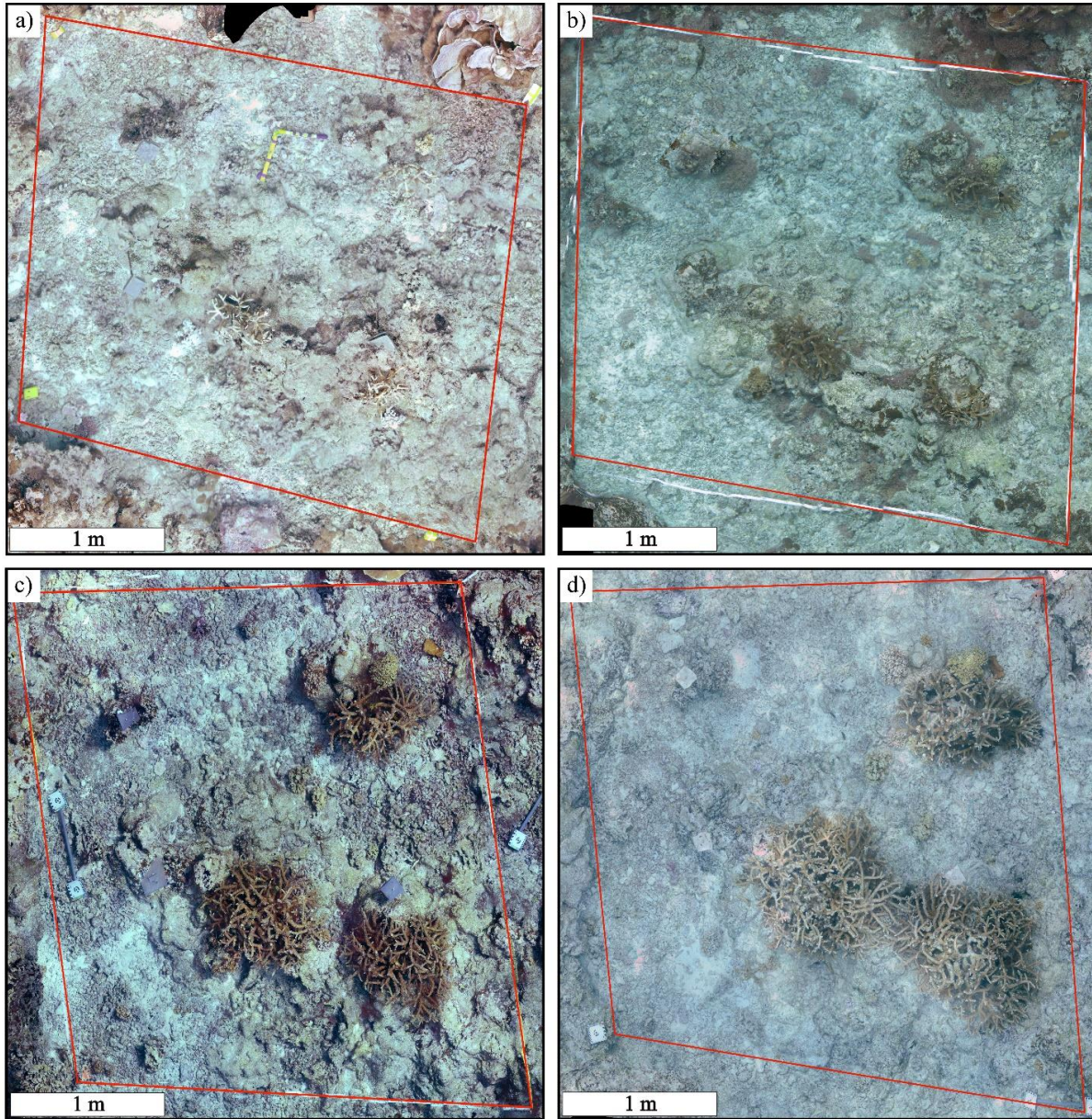


Figure 14. Orthophotos of a representative removal + transplants aggregated across species (XSP) treatment plot across time in September 2015 (top left), June 2016 (top right), September 2017 (bottom left), and September 2018 (bottom right).

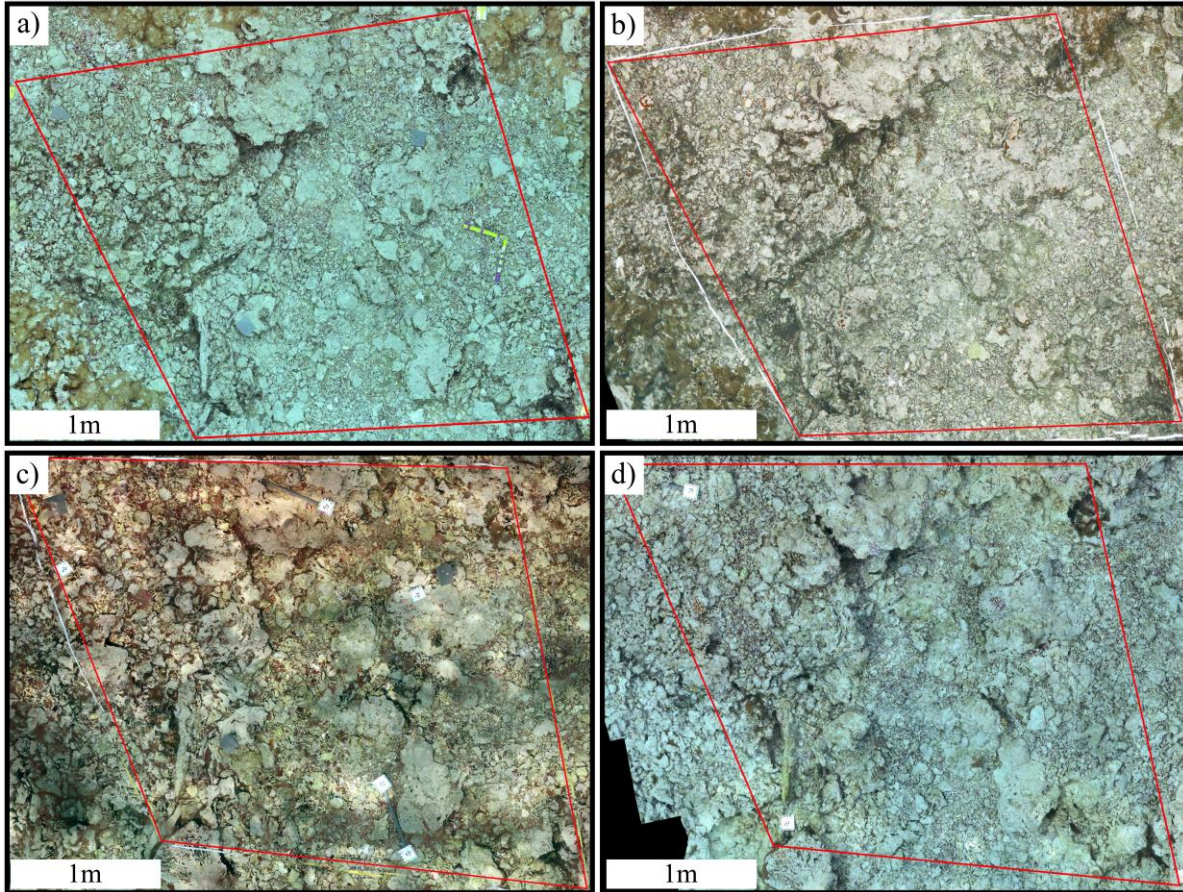


Figure 15. Orthophotos of a representative removal + no transplants (REM) treatment plot across time in September 2015 (top left), June 2016 (top right), September 2017 (bottom left), and September 2018 (bottom right).

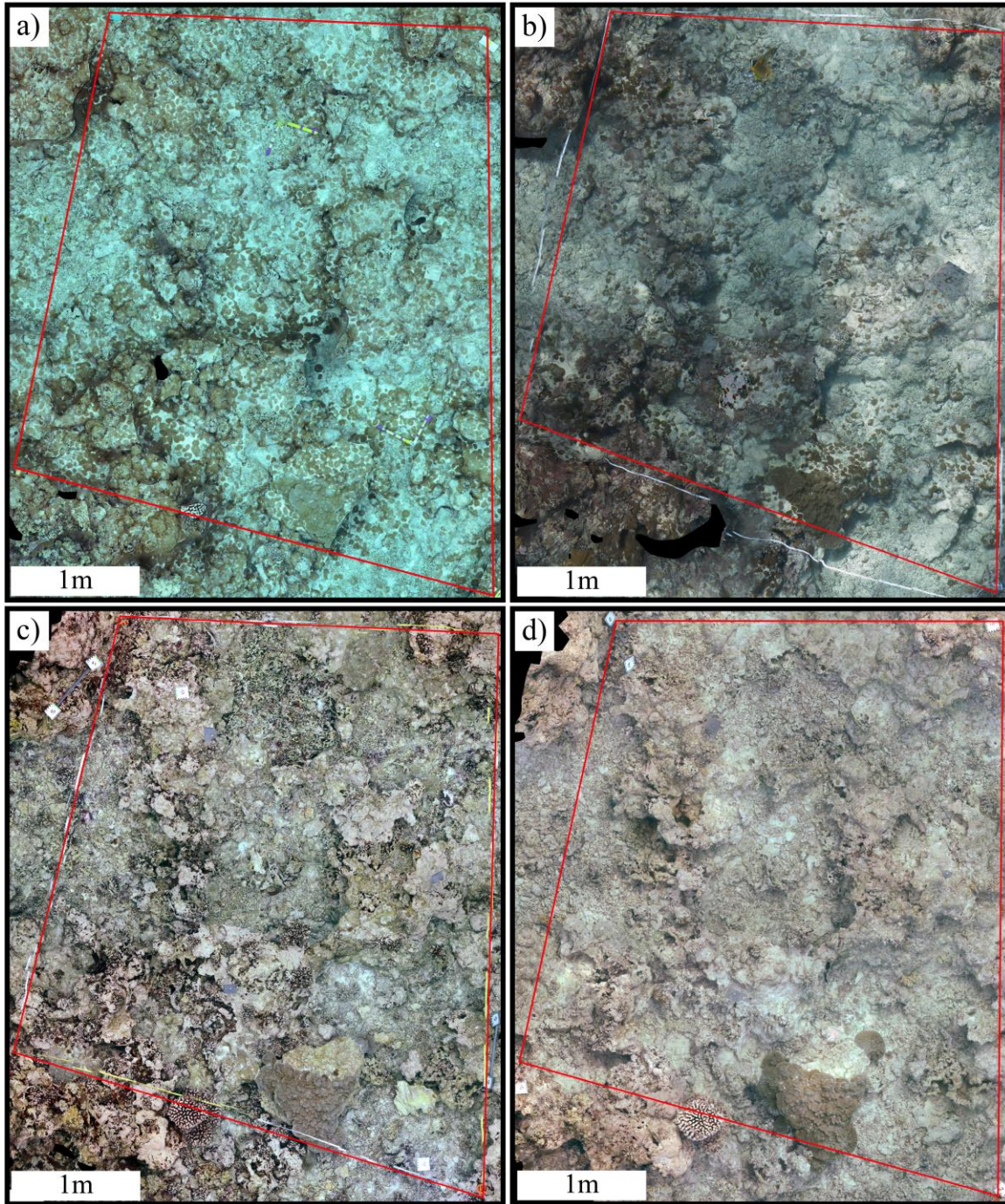


Figure 16. Orthophotos of a representative no removal + no transplants (CON) treatment plot across time in September 2015 (top left), June 2016 (top right), September 2017 (bottom left), and September 2018 (bottom right).

This thesis, in full, is currently being prepared for submission for publication of the material. Amir, CG; Petrovic, V; Edwards, CB; Fox, MD; Pedersen, NE; Carter, AL;

Johnson, MD; Sandin, SA; Smith, JE. The thesis author was the primary investigator and author of this material.

REFERENCES

- Aburto-Oropeza, O., Erisman, B., Galland, G. R., Mascareñas-Osorio, I., Sala, E., & Ezcurra, E. (2011). Large recovery of fish biomass in a no-take marine reserve. *PLoS ONE*, *6*(8), e23601. <https://doi.org/10.1371/journal.pone.0023601>
- Adam, T. C., Schmitt, R. J., Holbrook, S. J., Brooks, A. J., Edmunds, P. J., Carpenter, R. C., & Bernardi, G. (2011). Herbivory, connectivity, and ecosystem resilience: Response of a coral reef to a large-scale perturbation. *PLoS ONE*, *6*(8), e23717.
- Baird, A. H., & Hughes, T. P. (2000). Competitive dominance by tabular corals: An experimental analysis of recruitment and survival of understorey assemblages. *Journal of Experimental Marine Biology and Ecology*, *251*(1), 117–132. [https://doi.org/10.1016/S0022-0981\(00\)00209-4](https://doi.org/10.1016/S0022-0981(00)00209-4)
- Bellwood, D. R., Hughes, T. P., Folke, C., & Nyström, M. (2004). Confronting the coral reef crisis. *Nature*, *429*(6994), 827–833.
- Brito-Millán, M., Werner, B. T., Sandin, S. A., & McNamara, D. E. (2019). Influence of aggregation on benthic coral reef spatio-temporal dynamics. *Royal Society Open Science*, *6*(2), 181703. <https://doi.org/10.1098/rsos.181703>
- Buss, L. W., & Jackson, J. B. C. (1979). Competitive Networks: Nontransitive Competitive Relationships in Cryptic Coral Reef Environments. *The American Naturalist*, *113*(2), 223–234. <https://doi.org/10.1086/283381>
- Carlson, D. B., & Olson, R. R. (1993). Larval dispersal distance as an explanation for adult spatial pattern in two Caribbean reef corals. *Mar. Biol. Ecol*, *173*(2), 247–263.
- Carter, A. L., Edwards, C. B., Fox, M. D., Amir, C. G., Eynaud, Y., Johnson, M. D., ... Smith, J. E. (2019). Changes in benthic community composition associated with the outbreak of the corallimorph, *Rhodactis howesii*, at Palmyra Atoll. *Coral Reefs*, 1–13. <https://doi.org/10.1007/s00338-019-01841-5>
- Chadwick-Furman, N. E., & Spiegel, M. (2005). Abundance and clonal replication in the tropical corallimorpharian *Rhodactis rhodostoma*. *Invertebrate Biology*, *119*(4), 351–360. <https://doi.org/10.1111/j.1744-7410.2000.tb00103.x>
- Cinner, J., Marnane, M. J., McClanahan, T. R., & Almany, G. R. (2006). Periodic Closures as Adaptive Coral Reef Management in the Indo-Pacific. *Ecology and Society*, *11*(1). Retrieved from <http://www.ecologyand>
- Clements, C. S., & Hay, M. E. (2019). Biodiversity enhances coral growth, tissue survivorship and suppression of macroalgae. *Nature Ecology and Evolution*, *3*, 178–182 |. <https://doi.org/10.1038/s41559-018-0752-7>
- Connell, J. H. (1978). Diversity in Tropical Rain Forests and Coral Reefs. *Science*, *199*(4335), 1302–1310.
- Connell, J. H., Hughes, T. P., Wallace, C. C., Tanner, J. E., Harms, K. E., & Kerr, A. M. (2004). A LONG-TERM STUDY OF COMPETITION AND DIVERSITY OF CORALS. *Ecological Monographs*, *74*(2), 179–210.
- Darling, E. S., Alvarez-Filip, L., Oliver, T. A., McClanahan, T. R., & Côté, I. M. (2012). Evaluating life-history strategies of reef corals from species traits. *Ecology Letters*, *15*(12), 1378–1386. <https://doi.org/10.1111/j.1461-0248.2012.01861.x>
- De'ath, G., Fabricius, K. E., Sweatman, H., & Puotinen, M. (2012). The 27-year decline of coral cover on the Great Barrier Reef and its causes. *Proceedings of the National Academy of Sciences of the United States of America*, *109*(44), 17995–17999.

- <https://doi.org/10.1073/pnas.1208909109>
- Diaz-Pulido, G., McCook, L. J., Dove, S., Berkelmans, R., Roff, G., Kline, D. I., ... Hoegh-Guldberg, O. (2009). Doom and Boom on a Resilient Reef: Climate Change, Algal Overgrowth and Coral Recovery. *PLoS ONE*, 4(4), e5239.
<https://doi.org/10.1371/journal.pone.0005239>
- Dizon, R. M., & Yap, H. T. (2005). Coral responses in single- and mixed-species plots to nutrient disturbance. *Marine Ecology Progress Series*, 296, 165–172.
- Done, T. J. (1992). Phase shifts in coral reef communities and their ecological significance. *Hydrobiologia*, 247(1–3), 121–132.
- Edwards, C. B., Eynaud, Y., Williams, G. J., Pedersen, N. E., Zgliczynski, B. J., Gleason, A. C. R., ... Sandin, S. A. (2017). Large-area imaging reveals biologically driven non-random spatial patterns of corals at a remote reef. *Coral Reefs*, 36(4), 1291–1305.
<https://doi.org/10.1007/s00338-017-1624-3>
- Fine, M., & Loya, Y. (2003). Alternate coral-bryozoan competitive superiority during coral bleaching. *Marine Biology*, 142(5), 989–996. <https://doi.org/10.1007/s00227-002-0982-7>
- Forrester, G. E., Ferguson, M. A., O’Connell-Rodwell, C. E., & Jarecki, L. L. (2014). Long-term survival and colony growth of *Acropora palmata* fragments transplanted by volunteers for restoration. *Aquatic Conservation: Marine and Freshwater Ecosystems*, 24(1), 81–91. <https://doi.org/10.1002/aqc.2374>
- Forrester, G. E., Maynard, A., Schofield, S., & Taylor, K. (2012). Evaluating causes of transplant stress in fragments of *Acropora Palmata* used for coral reef restoration. *Bulletin of Marine Science*, 88(4), 1099–1113. <https://doi.org/10.5343/bms.2012.1016>
- Fox, M. D., Carter, A. L., Edwards, C. B., Takeshita, Y., Johnson, M. D., Petrovic, V., ... Smith, J. E. (2019). Limited coral mortality following acute thermal stress and widespread bleaching on Palmyra Atoll, central Pacific. *Coral Reefs*, 1–12.
<https://doi.org/10.1007/s00338-019-01796-7>
- Gardner, T. A., Côté, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2003). Long-term region-wide declines in Caribbean corals. *Science*, 301(5635), 958–960.
<https://doi.org/10.1126/science.1086050>
- Grottoli, A. G., Rodrigues, L. J., & Palardy, J. E. (2006). Heterotrophic plasticity and resilience in bleached corals. *Nature*, 440(7088), 1186–1189.
<https://doi.org/10.1038/nature04565>
- Guest, J. R., Dizon, R. M., Edwards, A. J., Franco, C., & Gomez, E. D. (2011). How Quickly do Fragments of Coral “Self-Attach” after Transplantation? *Restoration Ecology*, 19(2), 234–242. <https://doi.org/10.1111/j.1526-100X.2009.00562.x>
- Harrington, L. (2004). *Ecology of Crustose Coralline Algae; Interactions with Scleractinian Corals and Responses to Environmental Conditions*. James Cook University.
- Hein, M. Y., Willis, B. L., Beeden, R., & Birtles, A. (2017). The need for broader ecological and socioeconomic tools to evaluate the effectiveness of coral restoration programs. *Restoration Ecology*, 25(6), 873–883. <https://doi.org/10.1111/rec.12580>
- Heyward, A. J., & Negri, A. P. (1999). Natural inducers for coral larval metamorphosis. *Coral Reefs*, 18, 273–279.
- Highsmith, R. (1982). Reproduction by Fragmentation in Corals. *Marine Ecology Progress Series*, 7(4), 207–226. <https://doi.org/10.3354/meps007207>
- Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., ... Hatziolos, M. E. (2007). Coral reefs under rapid climate change and ocean

- acidification. *Science*, 318(5857), 1737–1742. <https://doi.org/10.1126/science.1152509>
- Hughes, Terence P., Rodrigues, M. J., Bellwood, D. R., Ceccarelli, D., Hoegh-Guldberg, O., McCook, L., ... Willis, B. (2007). Phase Shifts, Herbivory, and the Resilience of Coral Reefs to Climate Change. *Current Biology*, 17(4), 360–365. <https://doi.org/10.1016/j.cub.2006.12.049>
- Hughes, Terry P., Graham, N. A. J., Jackson, J. B. C., Mumby, P. J., & Steneck, R. S. (2010). Rising to the challenge of sustaining coral reef resilience. *Trends in Ecology and Evolution*, 25(11), 633–642. <https://doi.org/10.1016/j.tree.2010.07.011>
- Karlson, R. H., Cornell, H. V., & Hughes, T. P. (2007). Aggregation influences coral species richness at multiple spatial scales. *Ecology*, 88(1), 170–177. [https://doi.org/10.1890/0012-9658\(2007\)88\[170:AICSRA\]2.0.CO;2](https://doi.org/10.1890/0012-9658(2007)88[170:AICSRA]2.0.CO;2)
- Kelly, L. W., Barott, K. L., Dinsdale, E., Friedlander, A. M., Nosrat, B., Obura, D., ... Rohwer, F. (2012). Black reefs: Iron-induced phase shifts on coral reefs. *ISME Journal*, 6(3), 638. <https://doi.org/10.1038/ismej.2011.114>
- Knowlton, N., & Jackson, J. B. C. (2008). Shifting Baselines, Local Impacts, and Global Change on Coral Reefs. *PLoS Biology*, 6(2), e54. Retrieved from www.plosbiology.org
- Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecology Progress Series*, 323, 107–117.
- Kuguru, B. L., Mgay, Y. D., Öhman, M. C., & Wagner, G. M. (2004). The reef environment and competitive success in the Corallimorpharia. *Marine Biology*, 145(5), 875–884.
- Ladd, M. C., Miller, M. W., Hunt, J. H., Sharp, W. C., & Burkepile, D. E. (2018). Harnessing ecological processes to facilitate coral restoration. *Frontiers in Ecology and the Environment*, 16(4), 239–247. <https://doi.org/10.1002/fee.1792>
- Lester, S. E., Halpern, B. S., Grorud-Colvert, K., Lubchenco, J., Ruttenberg, B. I., Gaines, S. D., ... Warner, R. R. (2009). Biological effects within no-take marine reserves: A global synthesis. *Marine Ecology Progress Series*, 384, 33–46. <https://doi.org/10.3354/meps08029>
- Lirman, D., Thyberg, T., Herlan, J., Hill, C., Young-Lahiff, C., Schopmeyer, S., ... Drury, C. (2010). Propagation of the threatened staghorn coral *Acropora cervicornis*: Methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs*, 29(3), 729–735. <https://doi.org/10.1007/s00338-010-0621-6>
- Mccauley, D. J., Young, H. S., Guevara, R., Williams, G. J., Power, E. A., Dunbar, R. B., ... Micheli, F. (2014). Positive and Negative Effects of a Threatened Parrotfish on Reef Ecosystems. *Conservation Biology*, 28(5), 1312–1321. <https://doi.org/10.1111/cobi.12314>
- McClanahan, T. R., Uku, J. N., & Machano, H. (2002). Effect of macroalgal reduction on coral-reef fish in the Watamu Marine National Park, Kenya. *Marine and Freshwater Research*, 53, 223–231. <https://doi.org/10.1071/MF01112>
- Morse, D. E., Hooker, N., Morse, A. N. C., & Jensen, R. A. (1988). Control of larval metamorphosis and recruitment in sym-patric agariciid corals. *Mar. Biol. Ecol.*, 116, 193–217.
- Mumby, P. J., & Steneck, R. S. (2008). Coral reef management and conservation in light of rapidly evolving ecological paradigms. *Trends in Ecology and Evolution*. <https://doi.org/10.1016/j.tree.2008.06.011>
- Muthiga, N., Nordemar, I., Nyström, M., McClanahan, T., Elfwing, T., Sala, E., ... Bergman,

- K. (2002). Responses of algae, corals and fish to the reduction of macroalgae in fished and unfished patch reefs of Glovers Reef Atoll, Belize. *Coral Reefs*, 19, 367–379. <https://doi.org/10.1007/s003380000131>
- Myrberg, A. A., Brahy, B. D., & Emery, A. R. (1967). Field Observations on Reproduction of the Damselfish, *Chromis multilineata* (Pomacentridae), with Additional Notes on General Behavior. *Copeia*, 819–827. <https://doi.org/10.2307/1441893>
- Naughton, P., Edwards, C., Petrovic, V., Kastner, R., Kuester, F., & Sandin, S. (2015). Scaling the Annotation of Subtidal Marine Habitats. In *Proceedings of the 10th International Conference on Underwater Networks & Systems*. <https://doi.org/10.1145/2831296.2831342>
- Norström, A. V., Nyström, M., Lokrantz, J., & Folke, C. (2009). Alternative states on coral reefs: Beyond coral-macroalgal phase shifts. *Marine Ecology Progress Series*, 376, 295–306. <https://doi.org/10.3354/meps07815>
- Nyström, M., Folke, C., & Moberg, F. (2000). Coral reef disturbance and resilience in a human-dominated environment. *Trends in Ecology and Evolution*, 15(10), 413–417. [https://doi.org/10.1016/S0169-5347\(00\)01948-0](https://doi.org/10.1016/S0169-5347(00)01948-0)
- Palmer, M. A., Zedler, J. B., & Falk, D. A. (1997). Ecological theory and restoration ecology. *Foundations of Restoration Ecology: Second Edition*, 5(4), 291–300. https://doi.org/10.5822/978-1-61091-698-1_1
- Pedersen, N. E., Edwards, C. B., Eynaud, Y., Gleason, A. C. R., Smith, J. E., & Sandin, S. A. (2019). The influence of habitat and adults on the spatial distribution of juvenile corals. *Ecography*, 42(10), 1703–1713. <https://doi.org/10.1111/ecog.04520>
- Petrovic, V., Gidding, A., Wypych, T., Kuester, F., Defanti, T. A., & Levy, T. E. (2011). Dealing with archaeology’s data avalanche. *IEEE Computer Society*, 44(7), 56–60. <https://doi.org/10.1109/MC.2011.161>
- Pratchett, M. S., Anderson, K. D., Hoogenboom, M. O., Widman, E., Baird, A. H., Pandolfi, J. M., ... Lough, J. M. (2015). Spatial, Temporal And Taxonomic Variation In Coral Growth—Implications for the Structure And Function of Coral Reef Ecosystems. *Oceanography and Marine Biology: An Annual Review*, 53, 215–295. <https://doi.org/10.1201/b18733-7>
- Riegl, B., & Piller, W. (2001). Cryptic tissues inside *Acropora* frameworks (Indonesia): a mechanism to enhance tissue survival in hard times while also increasing framework density. *Coral Reefs*, 20(1), 67–68.
- Rinkevich, B. (2008). Management of coral reefs: We have gone wrong when neglecting active reef restoration. *Marine Pollution Bulletin*, 56, 1821–1824. <https://doi.org/10.1016/j.marpolbul.2008.08.014>
- Roberts, C. M., Bohnsack, J. A., Gell, F., Hawkins, J. P., & Goodridge, R. (2001). Effects of Marine Reserves on Adjacent Fisheries. *Science*, 294(5548), 1920–1923. <https://doi.org/10.1126/science.294.5548.1920>
- Rogers, C. S., Fitz, H. C., Gilnack, M., Beets, J., & Hardin, J. (1984). Scleractinian coral recruitment patterns at Salt River submarine canyon, St. Croix, U.S. Virgin Islands. *Coral Reefs*, 3(2), 69–76. <https://doi.org/10.1007/BF00263756>
- Sandin, S. A., Smith, J. E., DeMartini, E. E., Dinsdale, E. A., Donner, S. D., Friedlander, A. M., ... Sala, E. (2008). Baselines and Degradation of Coral Reefs in the Northern Line Islands. *PLoS ONE*, 3(2), e1548. <https://doi.org/10.1371/journal.pone.0001548>
- Sleman, J. C., Boggs, G. S., Radford, B. C., & 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. *Restoration Ecology*, 13(4), 685–694. <https://doi.org/10.1111/j.1526-100X.2005.00087.x>
- Smith, J. E., Smith, C. M., & Hunter, C. L. (2001). An experimental analysis of the effects of herbivory and nutrient enrichment on benthic community dynamics on a Hawaiian reef. *Coral Reefs*, 19(4), 332–342. <https://doi.org/10.1007/s003380000124>
- Smith, Jennifer E., Brainard, R., Carter, A., Grillo, S., Edwards, C., Harris, J., ... Sandin, S. (2016). Re-evaluating the health of coral reef communities: Baselines and evidence for human impacts across the central pacific. *Proceedings of the Royal Society B: Biological Sciences*, 283(1822), 20151985. <https://doi.org/10.1098/rspb.2015.1985>
- Smith, Jennifer E., Hunter, C. L., & Smith, C. M. (2010). The effects of top-down versus bottom-up control on benthic coral reef community structure. *Oecologia*, 163(2), 497–507. <https://doi.org/10.1007/s00442-009-1546-z>
- Steffen, W., Broadgate, W., Deutsch, L., Gaffney, O., & Ludwig, C. (2015). The trajectory of the Anthropocene: The Great Acceleration. *Anthropocene Review*, 2(1), 81–98. <https://doi.org/10.1177/2053019614564785>
- Steffen, W., Crutzen, P. J., & McNeill, J. R. (2007). The Anthropocene: Are Humans Now Overwhelming the Great Forces of Nature. *AMBIO: A Journal of the Human Environment*, 36(8), 614–621. [https://doi.org/10.1579/0044-7447\(2007\)36\[614:taahno\]2.0.co;2](https://doi.org/10.1579/0044-7447(2007)36[614:taahno]2.0.co;2)
- Tanner, J. E. (1996). Seasonally and lunar periodicity in the reproduction of Pocilloporid corals. *Coral Reefs*, 15(1), 59–66. <https://doi.org/10.1007/BF01626077>
- Tebben, J., Motti, C. A., Siboni, N., Tapiolas, D. M., Negri, A. P., Schupp, P. J., ... Harder, T. (2015). Chemical mediation of coral larval settlement by crustose coralline algae. *Scientific Reports*, 5, 10803. <https://doi.org/10.1038/srep10803>
- Tilman, D. (2004). Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences*, 101(30), 10854–10861. <https://doi.org/10.1073/pnas.0403458101>
- Tilman, David. (1999). The ecological consequences of changes in biodiversity: A search for general principles. *Ecology*, 80(5), 1455–1474.
- Vermeij, M. J. A., DeBey, H., Grimsditch, G., Brown, J., Obura, D., DeLeon, R., & Sandin, S. A. (2015). Negative effects of gardening damselfish *Stegastes planifrons* on coral health depend on predator abundance. *Marine Ecology Progress Series*, 528, 289–296. <https://doi.org/10.3354/meps11243>
- Vitousek, P., Mooney, H. A., Lubchenco, J., & Mellilo, J. M. (1997). Human domination of earth. *Science*, 277(5325), 494–499. <https://doi.org/10.1126/science.277.5325.494>
- Wallace, C. C. (1985). Reproduction, recruitment and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology*, 88(3), 217–233. <https://doi.org/10.1007/BF00392585>
- Williams, I. D., Polunin, N. V. C., & Hendrick, V. J. (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. <https://doi.org/10.3354/meps222187>
- Work, T. M., Aeby, G. S., & Maragos, J. E. (2008). Phase shift from a coral to a corallimorph-dominated reef associated with a shipwreck on Palmyra Atoll. *PLoS ONE*,

- 3(8), e2989. <https://doi.org/10.1371/journal.pone.0002989>
- Work, T. M., Aeby, G. S., Neal, B. P., Price, N. N., Conklin, E., & Pollock, A. (2018). Managing an invasive corallimorph at Palmyra Atoll National Wildlife Refuge, Line Islands, Central Pacific. *Biological Invasions*, 20(8), 2197–2208. <https://doi.org/10.1007/s10530-018-1696-1>
- Yachi, S., & Loreau, M. (1999). Biodiversity and ecosystem productivity in a fluctuating environment: the insurance hypothesis. *Proceedings of the National Academy of Sciences of the United States of America*, 96(4), 1463–1468. Retrieved from <http://www.ncbi.nlm.nih.gov/pubmed/9990046>