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# Outplanted *Acropora cervicornis* enhances the fish assemblages of Southeast Florida

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Thesis of  
Ellen Dignon Goldenberg

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science  
M.S. Marine Biology

Nova Southeastern University  
Halmos College of Natural Sciences and Oceanography

May 2019

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HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

OUTPLANTED *ACROPORA CERVICORNIS* ENHANCES THE FISH  
ASSEMBLAGES OF SOUTHEAST FLORIDA

By

Ellen D. Goldenberg

Submitted to the Faculty of  
Halmos College of Natural Sciences and Oceanography  
in partial fulfillment of the requirements for  
the degree of Master of Science with a specialty in:

Marine Biology

Nova Southeastern University

May 2019

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## Abstract

*Acropora cervicornis*, commonly known as the staghorn coral has historically been a major contributor to reef structural complexity, providing habitat for many functionally important fish species throughout Florida and the Caribbean. Unfortunately, due to disease, bleaching, and local anthropogenic stressors, *A. cervicornis* populations have suffered drastic declines that have negatively impacted associated reef fish populations. In order to promote recovery, *A. cervicornis* fragments can be cultivated in nurseries and outplanted back onto reefs. This practice can effectively increase *A. cervicornis* abundance, but the long-term effects on local fish assemblages, and specifically functionally important grazing fishes, has not been assessed. Fish assemblages at natural (control) sites were compared to outplanted *A. cervicornis* sites in Southeast Florida. Fish surveys were conducted each summer at four locations from 2012 to 2017. Each location contained three outplanted *A. cervicornis* and one or two control sites. Outplant sites were defined by 50 *A. cervicornis* colonies in a 36 m<sup>2</sup> area. Control sites occupied the same area but did not contain outplanted colonies. The fish assemblage structure was assessed in terms of composition, demography, and functional temporal trends as well as with the increasing structural complexity of the outplanted corals, defined as total linear extension (TLE). Significant temporal trends were recorded for total fish abundance, grazer abundance, and diversity. Structural complexity (outplanted *A. cervicornis* measured in TLE m<sup>-2</sup>) was found to be a significant predictor of total fish abundance, grazer abundance and diversity. Fishes 2-5 cm total length were most numerous indicating that the outplant sites may be providing habitat for juvenile reef fishes, particularly algae consumers. These findings suggest that *A. cervicornis* restoration may be creating a positive feedback loop in which outplanted corals create habitat for grazing fishes that in turn reduce algae competition, potentially providing new habitat for coral settlement.

**Keywords:** coral, reef restoration, structural complexity, grazing, herbivory

## Introduction

Coral reefs are one of the most diverse and productive ecosystems on the planet, providing food and habitat for countless species of fishes and invertebrates. Coral reefs also provide valuable resources to humans including food, pharmaceuticals, coastal protection, and tourism (Brander et al. 2012; Pratchett et al. 2015; O'Rourke et al. 2016; Pascal et al. 2016; Beck et al. 2018), amassing a net worth of more than US \$36 billion per year (Spalding et al. 2017). However, over the past 30 years, marine ecosystems have been increasingly impacted by the effects of coastal development, overfishing, and climate change which have led to declines in coral health and cover (Jackson et al. 2014; Heron et al. 2016; Zaneveld et al. 2016; Hughes et al. 2017a; Hughes et al. 2017b). Over the next century coral loss may continue to decline by 70-99% globally as ocean temperatures continue to increase (Hoegh-Guldberg et al. 2018).

The coral reefs of Florida and the greater Caribbean have been some of the most impacted, with losses of the endemic species, *Acropora cervicornis* (staghorn coral) and *Acropora palmata* (elkhorn coral) as great as 95% since the 1970s (Precht et al. 2002). These structurally complex, branching corals provide shelter to many species of reef fishes (Vargas-Angel et al. 2003). Their decline is due to an increased frequency of severe thermal events (Jaap and Sargent 1994) and a white-band disease event that persisted from the 1970s through the 1990s (Aronson and Precht 2001; Miller et al. 2002). These stressors have exacerbated the effect of natural threats such as hurricanes (Woodley et al. 1981; Lirman and Fong 1997) and predation (Knowlton et al. 1990). In 2006, *A. cervicornis* was listed as threatened under the US Endangered Species Act (ESA), and in 2008 it was determined to be critically endangered by the International Union for Conservation of Nature (IUCN) (Hogarth 2006; Aronson et al. 2008; Enochs et al. 2014).

The loss of *A. cervicornis* and other important framework-building corals has contributed to a decline in the distribution, abundance, and functional diversity of reef-associated fishes (Lirman 1999; Lemoine and Valentine 2012; Hernández-Delgado et al. 2014). Reef fish abundance and diversity are positively correlated with live coral cover (Carpenter et al. 1981; Ault and Johnson 1998). However, structural complexity provides shelter from predators and orientation points for physical communication, and may actually be a better predictor of fish abundance and species richness (Luckhurst and Luckhurst 1978; Roberts and Ormond 1987;

Gratwicke and Speight 2005; Walker et al. 2009; Agudo-Adriani et al. 2016; Darling et al. 2017). Structural complexity is often strongly positively associated with live coral cover, and the live tissue may be crucial for maintaining complexity long-term (Darling et al. 2017). Damselfish density was 65% higher on live *A. cervicornis* than on coral rubble (Wilkes et al. 2008), and survivorship of juvenile fishes was found to be significantly higher in the presence of structurally complex Acroporid corals (Beukers and Jones 1997; Quinn and Kojis 2007). The branching morphology of *A. cervicornis* creates a three-dimensional structure which provides valuable fish habitat, thus contributing to reef biodiversity (Vargas-Angel et al. 2003; Quinn and Kojis 2007; Mercado-Molina et al. 2015).

Reef fishes play an important role on coral reefs, and have immense economic and ecological importance (Brandt et al. 2009). The reef fish assemblages of Florida and the Caribbean are largely dominated by wrasses (Labridae), grunts (Haemulidae), damselfishes (Pomacentridae), parrotfishes (Scaridae) and surgeonfishes (Acanthuridae) (Ferro et al. 2005; Arena et al. 2007; Grober-Dunsmore et al. 2007; Kilfoyle et al. 2015; Broadman and Cummins 2016). These fish families fill a variety of functional roles that collectively promote reef health through nutrient cycling and algae removal (Hobson 1991; Burkepile and Hay 2011; Adam et al. 2015; Froese and Pauly 2018). Grazers, such as parrotfishes and surgeonfishes, are critically important because they directly reduce competition between coral and macroalgae for space on coral reefs (Hughes et al. 2007).

In recent years, many ecologically important species have been steadily disappearing from Florida and Caribbean reefs (Jackson et al. 2014; Cramer et al. 2017). A meta-analysis of reef fish abundance throughout the Caribbean found an overall decline as great as 2-6% per year (Paddack et al. 2009). One of the greatest sources of reduction in fish density has been the overexploitation of many coral reef species, and grazers have been some of the most impacted (Hughes 1994; Steneck 1994; Jackson et al. 2001; Paddack et al. 2009). Overfishing, coupled with the loss of stony corals, which serve as a crucial recruitment habitat for many species of juvenile fishes, and provide food and shelter to adult fishes, has led to tremendous declines in fish biodiversity (Jones et al. 2004; IUCN 2017).

The global decline of coral reefs and associated reef fishes has increased the necessity of active management and restoration efforts that benefit the entire reef community. Throughout

Southeast Florida and the Caribbean, nearly 30 organizations are working to increase the abundance of *A. cervicornis* and locally introduce new genotypes by growing colonies in coral nurseries and outplanting them back to degraded reefs. *Acropora cervicornis* grows rapidly and can reproduce asexually through fragmentation, and thus has been targeted by restoration efforts. This method has been successfully implemented throughout southeast Florida and the Caribbean (Johnson et al. 2011; Young et al. 2012; Mercado-Molina et al. 2015; Schopmeyer et al. 2017; Goergen and Gilliam 2018). Coral fragments are initially clipped from wild *A. cervicornis* colonies and cultivated in land-based or *in situ* nurseries. Corals may be grown on a variety of different structures including: coral trees, lines, concrete blocks, rebar frames, and PVC arrays (Johnson et al. 2011; Nedimyer et al. 2011). When nursery colonies are large enough, generally between 5-15 cm of live tissue, fragments are clipped and outplanted to an area of available reef substrate. Outplant colonies are attached to the substrate using any combination of epoxy, masonry nails, and cable ties (Johnson et al. 2011; Hollarsmith et al. 2012; Goergen and Gilliam 2018). Outplanting efforts have helped to replenish the reefs of southeast Florida and the Caribbean with over 36,000 colonies (Schopmeyer et al. 2017).

The survival of outplanted *A. cervicornis* colonies has been directly linked to macroalgal cover, with the greatest outplant survivorship occurring at sites with the lowest macroalgae cover (van Woesik et al. 2018). This relationship stresses the importance of grazers on outplant reefs through their ability to actively remove harmful algae. However, outplanting *A. cervicornis* has the potential to create habitat for grazers and other fishes that in turn supports the corals by reducing competition for space and increasing recruitment and light availability (Aronson and Precht 2006).

Until recently, few restoration efforts have evaluated the ecosystem benefits of outplanting corals to degraded reefs, and specifically the effect on local fish assemblages. Huntington et al. (2017) compared fish assemblages on outplanted *A. cervicornis* in Puerto Rico and found that outplanting had no significant effect on fish abundance, biomass, or species richness. Conversely, in the Pacific, over 6000 *Acropora tenuis* colonies were outplanted off Akajima Island in Japan. Most surviving corals matured after four years, and an abundance of small fishes and crustaceans were observed on the outplanted colonies (Omori and Iwao 2014). In the Philippines, fish species richness, diversity, and abundance were significantly higher on

outplanted *Acropora* spp. reefs than control reefs. (Cabaitan et al. 2008; Yap 2009). Similar positive associations between fish abundance and the addition of outplanted Acroporid corals have been observed throughout the Caribbean. A coral restoration effort in St. Croix, US Virgin Islands, found that the addition of *A. cervicornis* significantly increased reef rugosity, and outplanting, was specifically found to be a strong predictor of fish abundance and species richness (Opel et al. 2017). In Puerto Rico, *A. cervicornis* was outplanted on reefs that were severely damaged by ship groundings. The fish assemblages on the restored reefs were more similar to reference reefs than non-restored sites and contained a greater abundance of juvenile fishes (Nemeth et al. 2016).

Despite the possible benefits of active reef restoration, recovery remains a lengthy process. In the absence of disturbance it may take a decade or more for a reef to return to a pre-disturbance state (Jaap 2000). A long-term study examining recovery after hurricanes in the Caribbean found that most reefs had not returned to a pre-disturbance state eight years after the event (Gardner et al. 2005). However, *Acropora* spp. may recover from disturbance more quickly than other stony corals due to its rapid growth (Lucas and Weil 2015). In 1979, two hurricanes, David and Frederic, passed over St. Croix, U.S. Virgin Islands damaging at least 100 colonies of *A. palmata*. Rogers et al. (1982) found that 50 percent of these colonies had healed after only one year. Post-hurricane assessments of *A. palmata* in the Yucatán Peninsula found a lag in recovery time, but after five years the reef had recovered considerably (Jordan-Dahlgren and Rodriguez-Martinez 1998)

This study uses five years of data (2012-2017) to evaluate the ecosystem benefits of outplanting *A. cervicornis* in Southeast Florida, and particularly how it relates to reef functionality. Other studies have examined the effects of *A. cervicornis* restoration on fish diversity and abundance, but for no more than two years (Huntington et al. 2017; Opel et al. 2017). Reef fishes across all life stages are capable of dispersing hundreds to thousands of meters from their primary habitat in search of food and resources (Corless et al. 1997). Therefore, the existing reef fishes may colonize the newly created habitat provided by the outplanted *A. cervicornis* colonies. The introduction of outplanted corals should also foster increased recruitment of juvenile fishes (Shaish et al. 2010; Hernández-Delgado et al. 2014). Over time, outplant colony growth will increase structural complexity and is expected to attract a broad

range of species, sizes, and functional groups of fishes. This study examined long-term impacts of *A. cervicornis* restoration on total fish abundance, size class distribution, grazer abundance, and diversity as a result of changes in structural complexity and time in Southeast Florida.

## Methodology

This study utilized long-term fish count data collected at four *A. cervicornis* outplant locations offshore Broward County, Southeast Florida (Table 1). Each location was established in 2012 for the purpose of enhancing the wild population of *A. cervicornis* and to determine best outplanting practices in Southeast Florida. All locations were selected along the Nearshore Ridge Complex, which is composed of a series of shallow ridges lying inshore of the Inner Reef at approximately 3-6 m depth (Figure 1) (Walker et al. 2008). Large patches of *A. cervicornis* have historically and currently been found along this area of reef (Vargas-Angel et al. 2003; Walker et al. 2012; D'Antonio et al. 2016).

Table 1. Site name, depth, GPS coordinates, and date of outplanting.

| Location | Depth (m) | Latitude (°N) | Longitude (°W) | Date of Outplanting |
|----------|-----------|---------------|----------------|---------------------|
| Core 1   | 4.57      | 26.000833     | -80.107900     | 4/1/2012            |
| Core 2   | 4.23      | 26.014350     | -80.106733     | 4/1/2012            |
| Core 3   | 3.05      | 26.171200     | -80.089700     | 3/1/2012            |
| Core 4   | 3.66      | 26.179383     | -80.089083     | 3/1/2012            |

All four outplant locations were established in March or April 2012 (Figure 1). Each location was characterized by low-relief pavement colonized by reef biota such as sponges, encrusting zoanthids and macroalgae (Moyer et al. 2003; Gilliam et al. 2016). Outplant locations were divided into five different reef sites running south to north. Sites were defined by 36 m<sup>2</sup> areas of substrate, spaced 20 m apart (Figure 2). The northern and southernmost sites were established as controls where no outplanting occurred, and the three inner sites included 50 nursery-reared colonies of *A. cervicornis*. All colonies were outplanted with 5-15 cm of total live tissue, and each colony was marked by a cattle tag which aided in future determination of site boundaries. Control sites were marked by a galvanized nail in the center of the study area, and the 36 m<sup>2</sup> area was approximated by the diver during each fish survey.

Cryptic fish surveys were conducted to estimate the size and species of fishes within each site. This method was employed as it focused on the fishes utilizing structure rather than all fishes in the water column passing through the area (Agudo-Adriani et al. 2016). It is also a better way to observe juvenile and small adult fishes utilizing the outplanted colonies without harming the reef with piscicides (Brock 1982; Allen et al. 1992). To complete the cryptic survey, divers slowly swam throughout the entirety of the outplant or control site and carefully examined the area for fishes (Lirman 1999; Chittaro and Sale 2003; Agudo-Adriani et al. 2016). Surveys were completed in 15 minutes or less. All fishes were identified to a species level when possible, and size was estimated and assigned to one of six classes: <2 cm, 2-5 cm, 5-10 cm, 10-20 cm, 20-50 cm or >50 cm total length (TL). Annual fish surveys were conducted in August or September from 2012 to 2017 during the daylight hours of 0900 to 1700 local time.

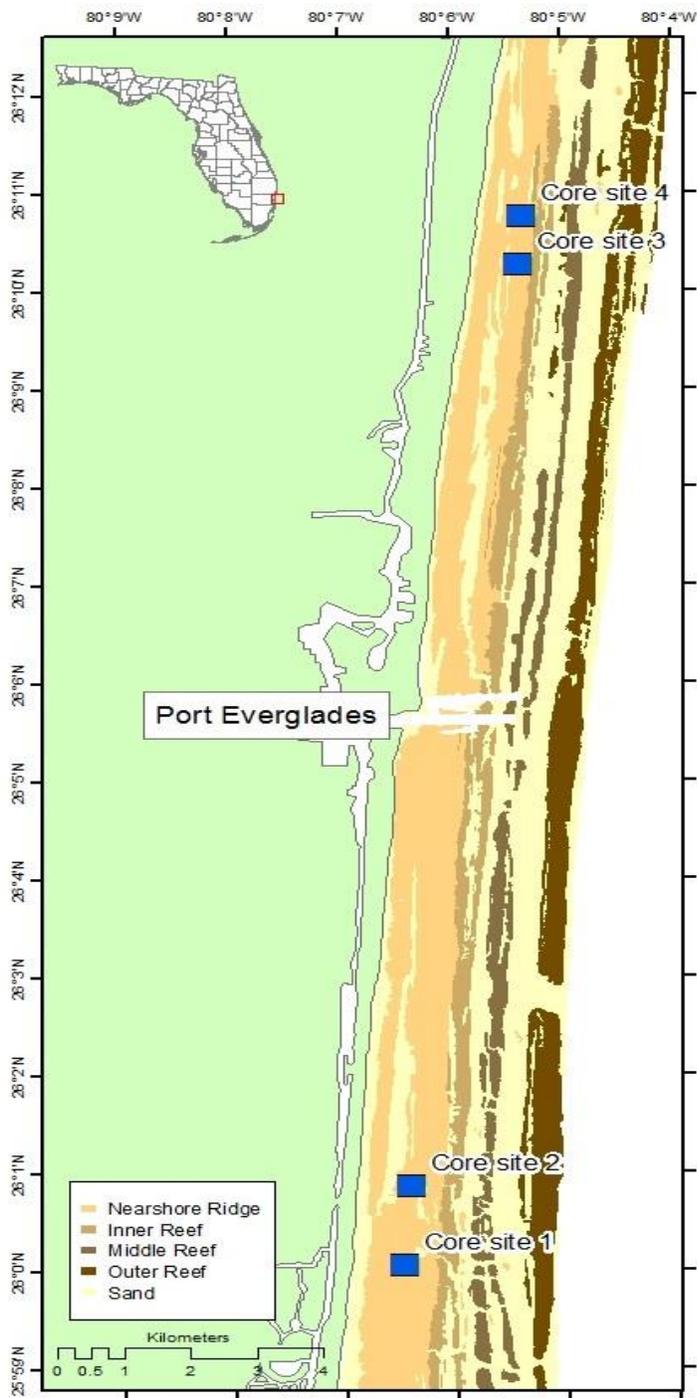


Figure 1. Map of study locations on the Nearshore Hardbottom Ridge habitat.

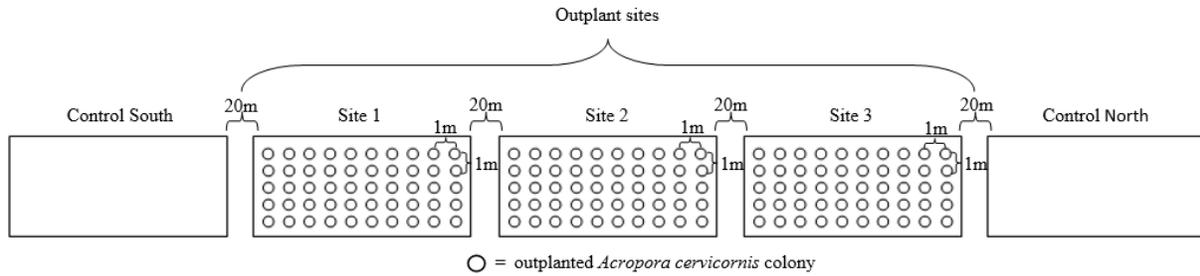


Figure 2. Outplant location layout depicting the distance between all sites as well as orientation of *Acropora cervicornis* fragments at each outplant site.

Throughout the project the outplant sites were impacted by three major hurricanes. In 2012, Hurricane Isaac passed offshore southwest of Broward County in late August (Berg 2013), and Hurricane Sandy passed to the east of Broward County in late October (Blake et al. 2013). Both storms produced significant wave energy that dislodged many outplanted colonies. Due to extreme colony losses, in early 2013 each outplant site was restocked with fragments of similar size to the remaining colonies.

Total linear extension (TLE), or the sum of all colony branch lengths, was used as a measure of the amount of structure contributed by the outplanted *A. cervicornis* across all sites (Kiel et al. 2012). Structural complexity data were not collected annually at the outplant sites, but colony counts were conducted up to five times per year from 2012 to 2016 and colony size class data were recorded at the time of outplanting and again in 2016 (Table 2). Structural complexity was not recorded in 2017 because Hurricane Irma damaged the outplant sites before such measurements could be made. In 2016, colonies were assigned into one of six size classes: 5-15 cm, 16-30 cm, 30-50 cm, 50-100 cm, 100-200 cm, or >200 TLE. The smallest value per size class was used for each colony so as not to overestimate TLE. Colony sizes were summed to obtain TLE per site using the equation:  $TLE = \Sigma (\text{Number of outplanted colonies in each size class} * \text{minimum colony size class value})$ .

Table 2. Dates of outplant colony counts and the number of colonies at each location. \*Colony counts were made after Hurricane Sandy. \*\*On May 13, 2013 missing colonies were replaced at all four locations.

| Date        | Site   |        |        |        | Grand Total |
|-------------|--------|--------|--------|--------|-------------|
|             | Core 1 | Core 2 | Core 3 | Core 4 |             |
| 5/25/2012   | 146    | 133    | 140    | 129    | 548         |
| 6/1/2012    | 149    | 149    | 149    | 141    | 588         |
| 6/29/2012   | 141    | 131    | 146    | 124    | 542         |
| 7/27/2012   | 140    | 130    | 146    | 124    | 540         |
| 9/7/2012    | 81     | 92     | 124    | 93     | 390         |
| Post Sandy* | 75     | 86     | NA     | NA     | NA          |
| 4/16/2013   | 74     | 85     | 70     | 66     | 295         |
| 5/13/13**   | 150    | 149    | 150    | 150    | 599         |
| 6/1/2013    | 147    | 149    | 141    | 144    | 581         |
| 8/1/2013    | 147    | 149    | 137    | 144    | 577         |
| 10/1/2013   | 147    | 149    | 137    | 144    | 577         |
| 2/1/2014    | 142    | 141    | 123    | 134    | 540         |
| 5/1/2014    | 140    | 141    | 119    | 131    | 531         |
| 8/1/2014    | 139    | 139    | 118    | 130    | 526         |
| 10/1/2014   | 133    | 137    | 113    | 127    | 510         |
| 2/1/2015    | 124    | 124    | 106    | 118    | 472         |
| 5/1/2015    | 119    | 120    | 104    | 111    | 454         |
| 8/1/2015    | 118    | 118    | 103    | 107    | 446         |
| 6/1/2016    | 79     | 59     | 77     | 57     | 272         |

### Data Analysis

All data analysis was conducted in R Statistical Software version 3.3.1 (R Core Team 2016). Mean fish abundance was calculated per year across all outplant sites, and species richness was determined as the average number of species recorded per site. Due to site setup constraints in 2012 and the availability of appropriate habitat, several locations had only one control site. Additionally, during multiple survey events only one control site was sampled at locations that had two established control sites. Therefore, only one control site per location was used for data analysis each year. Where data were collected on both control sites, one was randomly selected using R Statistical Software (R Core Team 2016) (Table 3). However, in 2012, 125 juvenile grunts were recorded at a control site at an outplant location that had two control sites, so the other control site was utilized for analysis. Mean fish abundance and the abundance of each size class was calculated by year across all four selected control sites.

Similarly, species richness was determined as the mean number of recorded species across each designated control site.

Table 3. Table of randomly selected control sites. Control sites were considered fixed at locations with only one control site, or if cryptic fish surveys were only collected at one control site at a location with two control sites. Control sites were considered random if data were collected at both control sites at a given location and one control site had to be randomly selected with the use of R Statistical Software. The south control at Core 2 in 2012 was considered fixed because a school of 125 juvenile grunts passed through the north control that year.

| <b>Year</b> | <b>Site</b> | <b>Control</b> | <b>Selection</b> |
|-------------|-------------|----------------|------------------|
| 2012        | 1           | South          | Fixed            |
| 2012        | 2           | South          | Fixed            |
| 2012        | 3           | North          | Fixed            |
| 2012        | 4           | South          | Random           |
| 2013        | 1           | South          | Fixed            |
| 2013        | 2           | North          | Random           |
| 2013        | 3           | North          | Random           |
| 2013        | 4           | North          | Random           |
| 2014        | 1           | South          | Fixed            |
| 2014        | 2           | South          | Random           |
| 2014        | 3           | North          | Random           |
| 2014        | 4           | North          | Fixed            |
| 2015        | 1           | South          | Fixed            |
| 2015        | 2           | South          | Random           |
| 2015        | 3           | South          | Random           |
| 2015        | 4           | South          | Random           |
| 2016        | 1           | South          | Fixed            |
| 2016        | 2           | North          | Random           |
| 2016        | 3           | North          | Random           |
| 2016        | 4           | North          | Random           |
| 2017        | 1           | South          | Fixed            |
| 2017        | 2           | South          | Random           |
| 2017        | 3           | South          | Random           |
| 2017        | 4           | North          | Random           |

All fishes were classified into seven functional groups based on classifications made by Newman et al. (2006) and used by Allgeier et al. (2014). These seven functional groups included: herbivore, macroinvertivore, microinvertivore, omnivore, piscivore, piscivore-invertivore, and planktivore. Classifications were made by consulting the literature, as well as IUCN Redlist (IUCN 2018) and FishBase (Froese and Pauly 2018). With the generally poor state

of reefs in South Florida and the Caribbean, this study focused on a functional group that is known to have direct benefits to coral reefs. Therefore, herbivores and omnivores were combined to form a 'grazer' functional group to encompass the role of macroalgae removal on coral reefs. Grazers were further divided into size classes and analyzed across outplant and control sites.

Regression analyses were conducted with time as the predictor variable for total fish abundance, all size classes, species richness, grazer abundance, and each size class of grazers per site at both control and outplant sites. Regression models were also used to examine the relationship between structural complexity (TLE,  $\text{cm m}^{-2}$ ) and total fish abundance, species richness, each size class of fishes, total grazer abundance and all size classes of grazers  $\text{m}^{-2}$  for 2016 alone across all 12 outplant sites. The data were analyzed with generalized additive models (GAMs). Differences between outplant and control sites were also assessed with GAMs.

## Results

From 2012 to 2017, a total of 5423 fishes from 23 families were identified in the summer cryptic fish surveys across all four locations (Appendix 1). There were 4213 fishes present at the outplant sites, and 987 fishes recorded on the control sites. Sixty-nine distinct taxa from 22 families were identified to species level at the outplant sites. Juvenile grunts (Haemulidae), several blennies (Blenniidae) and one parrotfish (Scaridae) could only be identified to family level. Forty-five species from 17 families were identified to the species level on the control sites. Juvenile grunts were identified to a family level (Haemulidae) and several blennies could only be identified as Blenniidae. The only family unique to the control sites was the family Muraenidae, which was represented by one recorded goldentail moray eel in 2017.

### Total Fish Abundance

There was a significant increase in total fish abundance over time on the outplant sites ( $p=0.00151$ ; GAM; Figure 3; Appendix 2), and a significant decreasing trend on the control sites ( $p=0.000174$ ; GAM; Figure 4; Appendix 2). Significant site level differences were recorded between outplant and control sites ( $p=0.0358$ ; GAM; Appendix 3). In 2016, a significant positive relationship was observed between structural complexity and fish abundance  $\text{m}^{-2}$  ( $p=0.000000863$ ; GAM; Figure 5; Appendix 4).

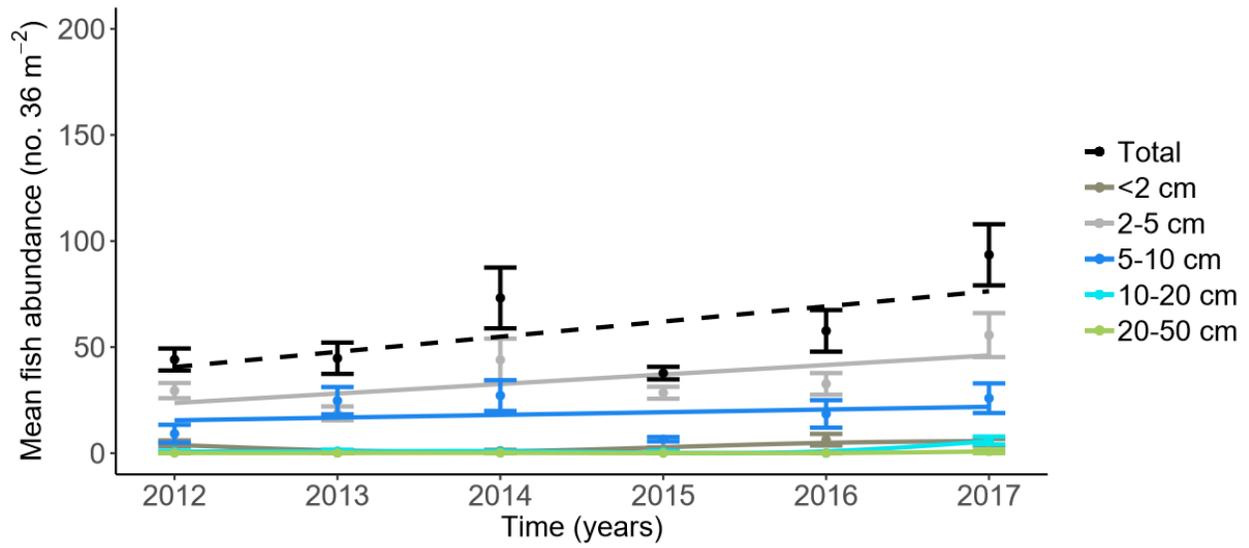


Figure 3. The temporal change in mean ( $\pm$ SE) fish abundance across all outplant sites (site = 36 m<sup>2</sup>).

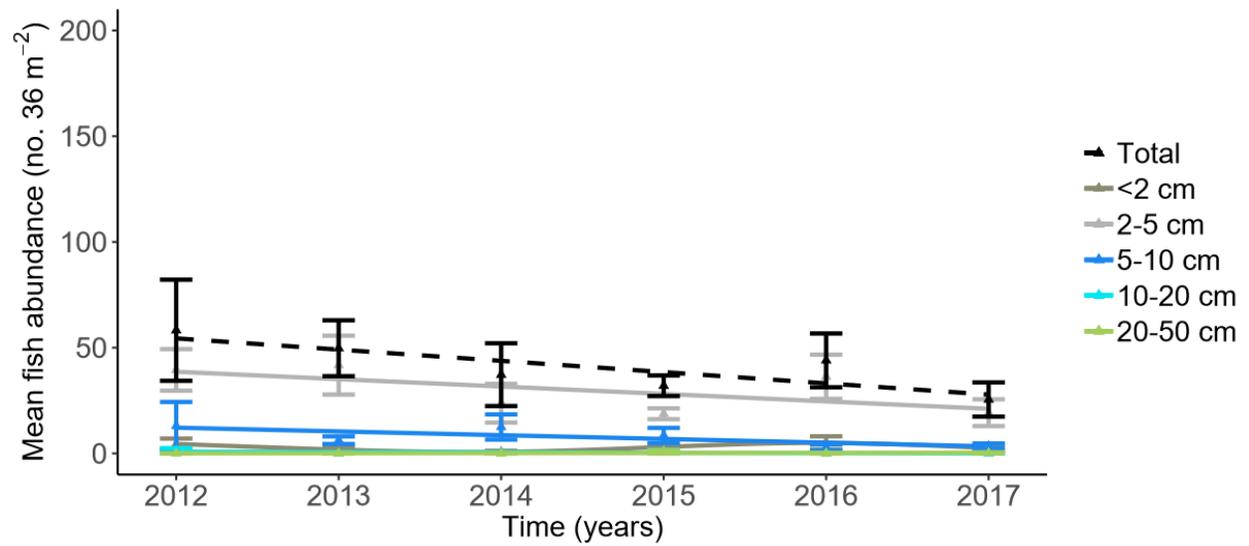


Figure 4. The temporal change in mean ( $\pm$ SE) fish abundance across four control sites (site = 36 m<sup>2</sup>).

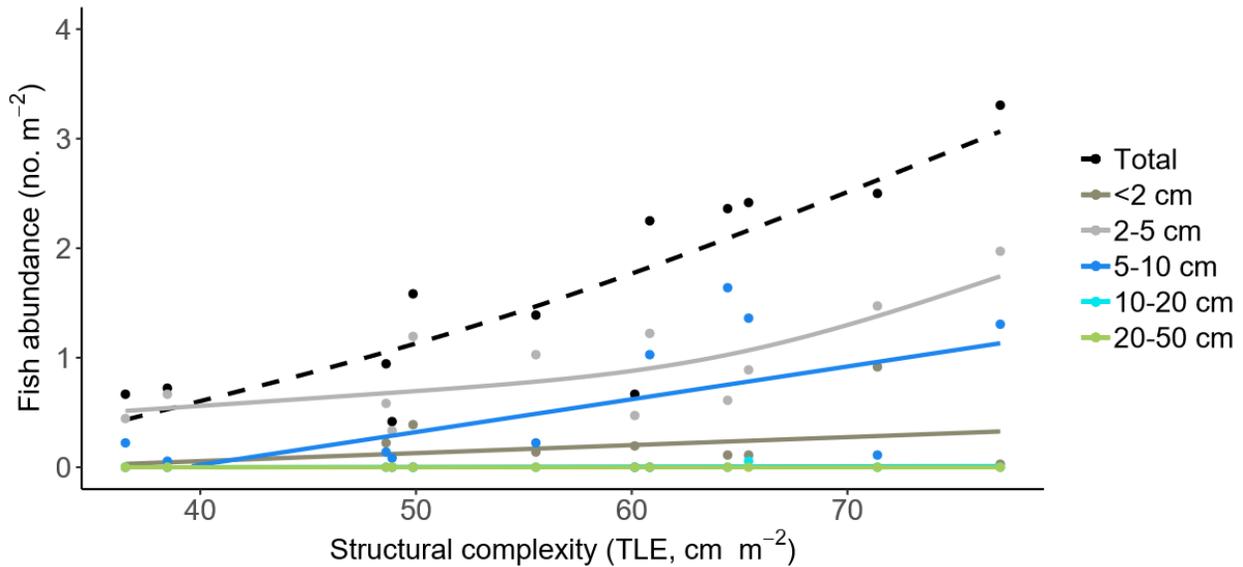


Figure 5. The relationship between fish abundance (no. m<sup>-2</sup>) and structural complexity (TLE, cm m<sup>-2</sup>) in 2016.

There was a significant increasing trend of fishes <2 cm TL at the outplant sites ( $p=0.0249$ ; GAM; Figure 3; Appendix 2), and significant decreasing temporal trend at the control sites ( $p=0.00657$ ; GAM; Figure 4; Appendix 2). However, the trends of fishes <2 cm TL at the outplant and control sites were not significantly different ( $p=0.563$ ; GAM; Appendix 3). In 2016, a positive relationship was observed between structural complexity and fishes <2 cm TL ( $p=0.0393$ ; GAM; Figure 5; Appendix 4).

The most abundant size class at both the outplant and control sites was the 2-5 cm TL size class. There was an increasing temporal trend of fish abundance within this size class at the outplant sites ( $p=0.00157$ ; GAM; Figure 3; Appendix 2) and decreasing trend at the control sites ( $p=0.00131$ ; GAM; Figure 4; Appendix 2). However, there were no site level differences recorded ( $p=0.423$ ; GAM; Appendix 3). In 2016, there was a significant, positive relationship between fishes 2-5 cm TL and structural complexity ( $p=0.00000619$ ; GAM; Figure 5; Appendix 4).

There was a significant increasing temporal trend in the abundance of fishes 5-10 cm TL at the outplant sites ( $p=0.00892$ ; GAM; Figure 3; Appendix 2) and significant decreasing trend at the control sites ( $p=0.00407$ ; GAM; Figure 4; Appendix 2). Site level differences were also recorded ( $p=0.00685$ ; GAM; Appendix 3). When compared to structural complexity in 2016,

there was a significant increase of fishes 5-10 cm TL at sites with greater structural complexity ( $p=0.00676$ ; GAM; Figure 5; Appendix 4).

The 10-20 cm ( $p=0.0693$ ; GAM) and 20-50 cm TL ( $p=0.0661$ ; GAM) fish size classes remained relatively stable between 2012 and 2016 and peaked in 2017 across the outplant sites (Figure 3; Appendix 2). No significant temporal trends were recorded for the 10-20 cm ( $p=0.13$ ; GAM) and 20-50 cm TL ( $p=0.267$ ; GAM) size classes across all control sites (Figure 4; Appendix 2). There was, however, a significant difference between outplant and control sites for fishes 10-20 cm TL ( $p=0.0412$ ; GAM; Appendix), but there was no significant relationship between fishes of this size class and structural complexity in 2016 ( $p=0.351$ ; GAM; Appendix). There was no difference between outplant and control sites for fishes 20-50 cm TL ( $p=0.932$ ; GAM; Appendix 3). No fishes greater than 50 cm were observed on either outplant or control sites throughout the duration of the project.

### **Species Richness**

There was a significant difference between outplant and control sites in terms of mean species richness ( $p=0.0319$ ; GAM; Appendix 3). At the outplant sites, species richness peaked in 2014, followed by a slight decline through 2016, and then increasing in 2017 ( $p=0.0000101$ ; GAM; Figure 6; Appendix 2). There was a significant decreasing temporal trend of mean species richness on the control sites ( $p=0.0000513$ ; GAM; Figure 7; Appendix 2). When compared to structural complexity, there was a positive relationship between species richness and structural complexity (TLE,  $\text{cm m}^{-2}$ ) in 2016 ( $p=0.000000649$ ; GAM; Figure 8; Appendix 4).

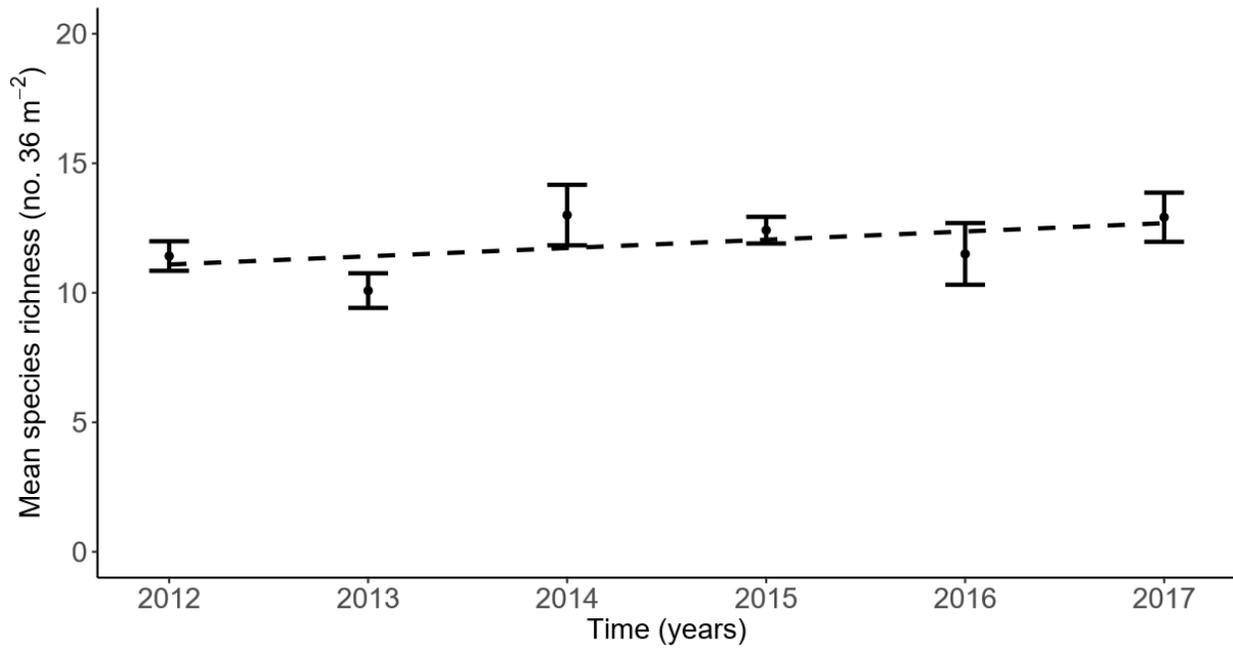


Figure 6. The temporal change in mean ( $\pm$ SE) species richness across all outplant sites (site = 36 m<sup>2</sup>).

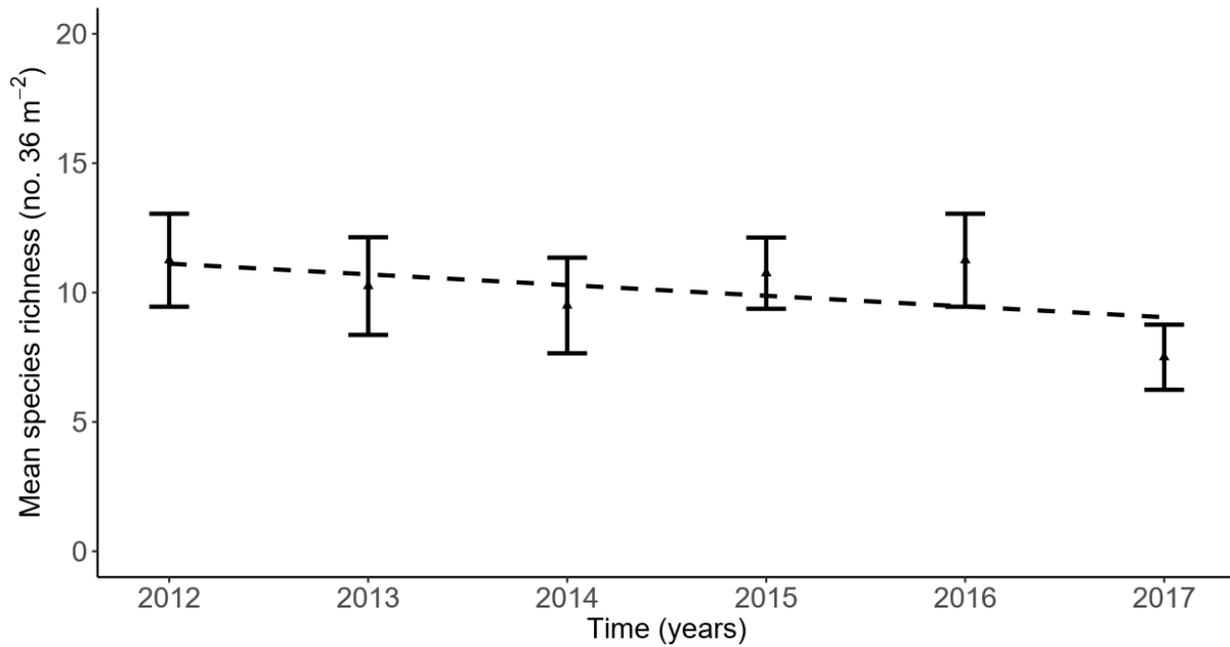


Figure 7. The temporal change in mean ( $\pm$ SE) species richness across four control sites (site = 36 m<sup>2</sup>).

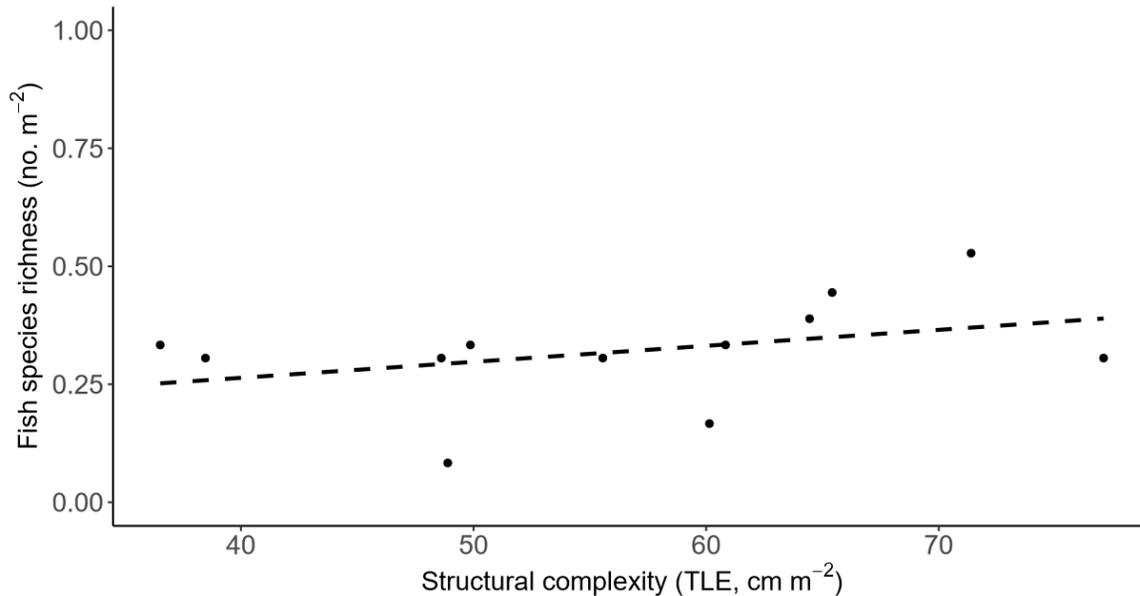


Figure 8. The relationship between species richness (no. m<sup>-2</sup>) and structural complexity (TLE, cm m<sup>-2</sup>) in 2016.

### Grazers

Grazer abundance increased significantly at the outplant sites ( $p=0.00754$ ; GAM; Figure 9; Appendix 2), and decreased significantly at the control sites ( $p=0.00355$ ; GAM; Figure 9; Appendix 2), but there was no site level difference between outplants and controls ( $p=0.0723$ ; GAM; Appendix 3). There was, however, a significant positive relationship between grazer abundance and structural complexity ( $p=0.00276$ ; exponential regression model; Figure 11; Appendix 4). Grazers 2-5 cm TL were most abundant, and there was a significant increase over time at the outplant sites ( $p=0.00405$ ; GAM; Figure 9; Appendix 2) and a significant decrease over time at the control sites ( $p=0.0102$ ; GAM; Figure 10; Appendix 2). The abundance of grazers 2-5 cm TL increased exponentially with structural complexity in 2016 ( $p=0.0119$ ; exponential regression model; Figure 11; Appendix 4).

There was a significant increasing temporal trend in the abundance of grazers <2 cm TL at the outplant sites ( $p=0.0379$ ; GAM; Figure 9; Appendix 2) and a significant decrease at the control sites ( $p=0.0405$ , GAM; Figure 10; Appendix 2). There was a significant relationship between grazers <2 cm TL and structural complexity at the outplant sites ( $p=0.0462$ ; GAM; Figure 11; Appendix 4), but there were no significant site level difference recorded between outplants and controls ( $p=0.914$ ; GAM; Appendix 3). There was a significant difference between outplant and control sites for grazers 5-10 cm TL ( $p=0.00332$ ; GAM; Appendix). The abundance

of grazers 5-10 cm TL increased over time at the outplant sites ( $p=0.0199$ ; GAM; Figure 9; Appendix 2) and with structural complexity ( $p=0.0163$ ; exponential regression model; Figure 11; Appendix 4). While grazers 5-10 cm TL decreased significantly at the control sites from 2012-2017 ( $p=0.00388$ ; GAM; Figure 10; Appendix 2). No significant relationship between mean abundance of fishes 10-20 cm TL and time was recorded at the outplant ( $p=0.0766$ ; GAM; Figure 9; Appendix 2) or control sites ( $p=0.111$ ; GAM; Figure 9; Appendix 2), however there was a significant difference at the site level ( $p=0.01651$ ; GAM; Appendix 3). There was also no significant relationship between grazers 10-20 cm TL and structural complexity ( $p=0.351$ ; GAM; Figure 11; Appendix). There was no relationship between grazers 20-50 cm TL and time at both outplant ( $p=0.0966$ ; GAM; Figure 9; Appendix 2) and control ( $p=0.418$ ; GAM; Figure 9; Appendix 2) sites, and no grazers over 20 cm TL were recorded in 2016

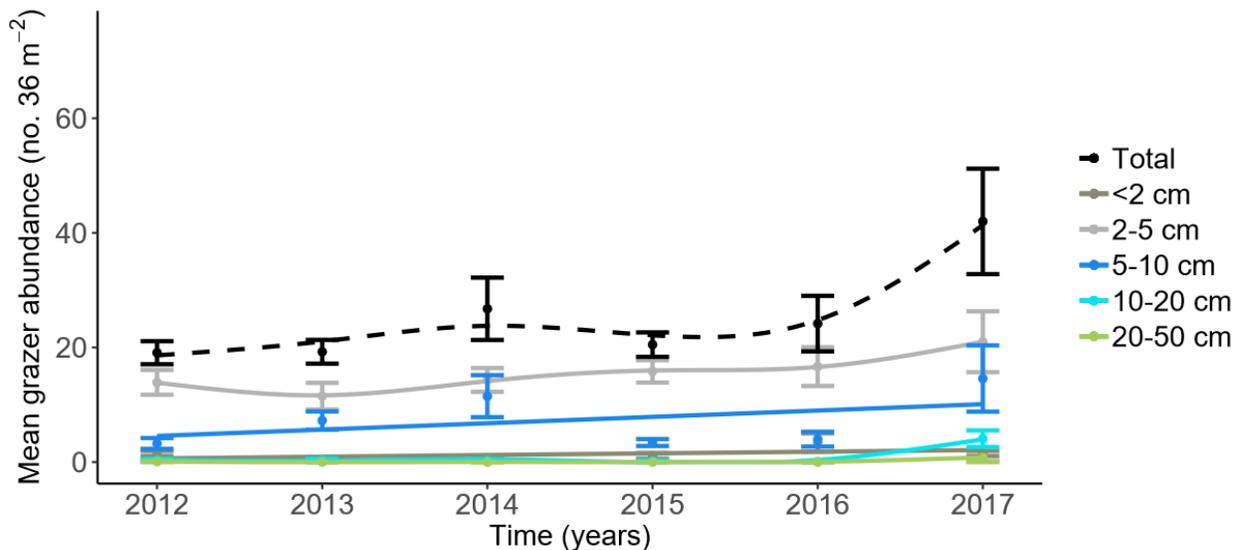


Figure 9. The temporal change in mean ( $\pm$ SE) grazer abundance across all outplant sites (site = 36 m<sup>2</sup>).

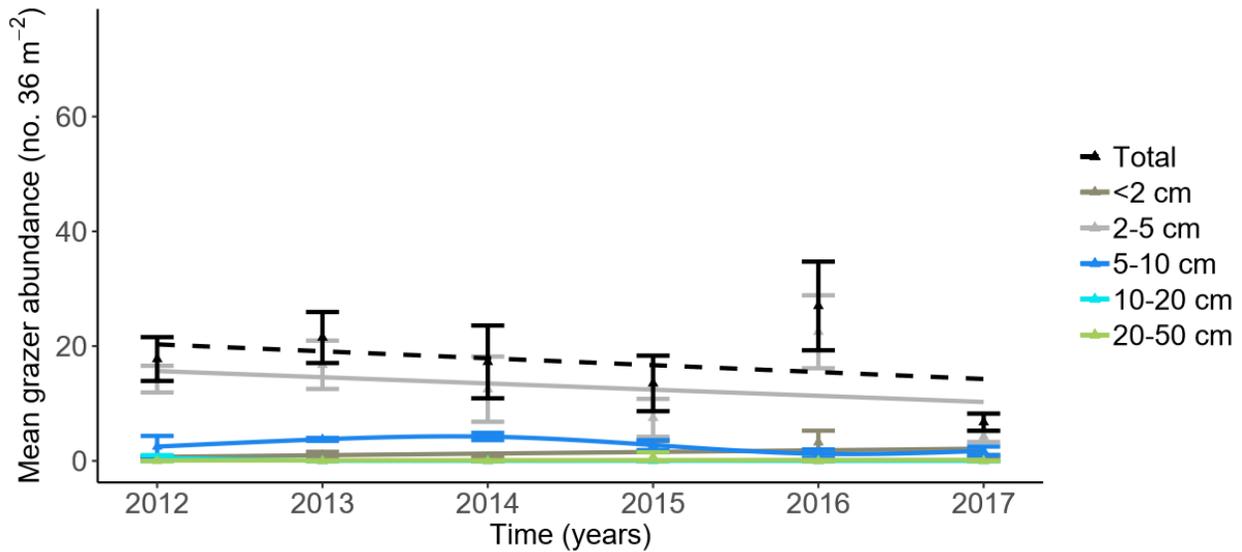


Figure 10. The temporal change in mean ( $\pm$ SE) grazer abundance across four control sites (site = 36 m<sup>2</sup>).

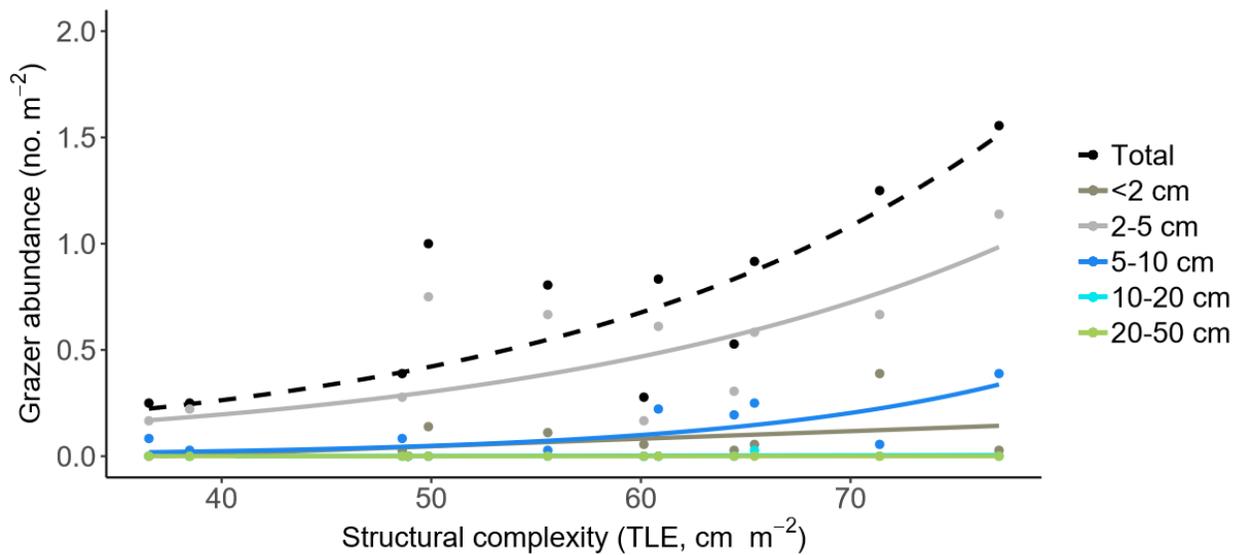


Figure 11. The relationship between grazer abundance (no. m<sup>-2</sup>) and structural complexity (TLE, cm m<sup>-2</sup>) in 2016.

## Discussion

This five-year study highlighted a change in the fish assemblage over time in terms of composition, demography, and functionality and identified specific differences between outplant and control sites. Fish abundance generally declined across the control sites and increased across the outplant sites. Fish abundance was greatest at outplant sites with the greatest structural

complexity which suggests that significant trends in fish abundance were likely due to the change in structural complexity (TLE,  $\text{cm m}^{-2}$ ) contributed by the outplanted *A. cervicornis*. This is further supported by the fact that TLE increased from 3000  $\text{cm m}^{-2}$  in 2012 to over 24000  $\text{cm m}^{-2}$  in 2016. The trend of fish abundance is consistent with Opel et al. (2017), which reported significantly more fish on outplant than control reefs. Opel et al. (2017) also noted an increase in species richness which was supported by the present study. The greatest fish abundance on the outplant sites was observed in the last year of the project. This may indicate that at least five years of coral growth are required to make an impact on the reef ecosystem, which is consistent with previous estimates of reef recovery time (Jordan-Dahlgreen and Rodriguez-Martinez 1998). However, it may simply be the result of the variability of fish counts and fish assemblages.

The decreasing trend of fish abundance across the control sites may be following the general decline of reef fishes throughout Florida and the Caribbean (Jackson et al. 2001; Paddock et al. 2009; Jackson et al. 2014). However, it is possible that the outplant sites may be functioning like an artificial reef in which they are attracting fish away from the nearby control sites due to the additional structure, rather than enhancing the reef by creating new habitat for recruitment which can increase biomass (Bohnsack 1989). Sites were established 20 m apart to reduce the chance of this happening, but this hypothesis was not actually tested. Declines in fish abundance at the control sites over time as well as the variation among the outplant sites may also be due to the natural variation of fish assemblages. Sampling was conducted at the same time each year to account for seasonal variation, but this study did not account for regular diel and lunar migrations of reef fishes. Grunts make daily migrations to specific reefs to feed and avoid predation (Ogden and Ehrlich 1977), bluehead wrasse migrate daily to spawn (Warner et al. 1975), parrotfish migrate between diel feeding areas and nocturnal resting areas (Ogden and Buckman 1973), and some reef fishes migrate around the full moon to spawn (Pressley 1980). These natural behaviors could easily skew a demographic fish survey.

There was an increase in juvenile reef fishes at the outplant sites during the study, which correlated with increasing structural complexity. Caribbean reef fish recruitment typically occurs during the spring or early summer (Munro et al. 1973; Luckhurst and Luckhurst 1977; Sponaugle and Cowen 1996,1997). Data were collected during the late summer which may partially explain why most of the individuals recorded were 5 cm TL or smaller. Many reef fishes regularly utilize

branching corals as nursery habitat (Tolimieri 1998; Adam et al. 2011). Huntington et al. (2017) reported that regional increases in fish abundance with greater *A. cervicornis* density were largely driven by smaller size classes, particularly of the Family Haemulidae. Within the present study there was a significant increase over time and with increasing structural complexity in both the <2 and 2-5 cm TL size classes. This finding suggests that the microhabitats created by *A. cervicornis* at the outplant sites may be serving as a habitat for juvenile and small adult fishes. (Precht et al. 2010; Agudo-Adriani et al. 2016).

Very few fishes were recorded over 10 cm TL. There was no temporal increase or increase with greater structural complexity for fishes greater than 10 cm TL. This is consistent with Lirman et al. (2010) which reported a low abundance of fishes greater than 20 cm TL on natural thickets of *A. cervicornis*. Similarly, Huntington et al. (2017) found no positive relationship between *A. cervicornis* density and fishes greater than 15 cm fork length. The general lack of fishes greater than 10 cm TL may be due to overfishing throughout Florida and the Caribbean (Hughes 1994; Jackson et al. 2001), or perhaps the type of habitat created by *A. cervicornis* is simply not suitable for larger fishes. Additionally, the relatively small sites (36 m<sup>2</sup>) may be too small to gain any statistical control over such a rare event as a large fish. Larger fishes are also more mobile and have lower site fidelity at the scale of the sites, which makes capturing any statistical signal challenging (Addis et al. 2007). It is also possible that five years was not ample time to allow the outplanted colonies to grow large enough to accommodate more fishes greater than 10 cm TL.

Some of the most commonly recorded fishes at the outplant sites were consistent with those found on natural *A. cervicornis* reefs. Haemulidae, Scaridae, Pomacentridae, Labridae, and Acanthuridae are often numerically dominant families on *A. cervicornis* reefs throughout the Caribbean. Commercially important families such as Lutjanidae (snappers) and Serranidae (groupers) are uncommon to rare (Lirman et al. 2010; Agudo-Adriani et al. 2016). Snapper abundance has been positively associated with the topographic complexity of Acroporid corals (Lirman 1999), but the low abundances recorded in the present study could not support this finding.

One of the most important findings from this study was the significant increase of grazer abundance over the course of the study and with increasing structural complexity. Grazers such

as sea urchins, surgeonfishes, and parrotfishes play a critical role on coral reefs. They aid in the removal of turf and macroalgae which compete with corals for space and resources (Adam et al. 2015). The reefs of Florida and the Caribbean have suffered a reduction of grazers due to a 1980s disease event that killed large numbers of the sea urchin, *Diadema antillarum* (Bak et al. 1984; Lessios et al. 1984; Lessios 1988). After the die-off, parrotfishes replaced urchins as the primary algae consumers on Caribbean coral reefs (Carpenter 1990; Aronson and Precht 2006; Mumby et al. 2006a), but parrotfish abundance has also declined over time from overfishing (Hughes 1994; Steneck 1994; Cramer et al. 2017). One of the most commonly recorded grazers on the outplant sites was the stoplight parrotfish (*Sparisoma viride*). Though truly an omnivore due to its regular consumption of live coral tissue, stoplight parrotfish may obtain up to 95% of their diet from algae (Bythell et al. 1993; Bruggemann et al. 1994; Adam et al. 2015; Froese and Pauly 2018). Juvenile stoplight parrotfish are known to use shallow areas dominated by *A. cervicornis* as nursery habitats (Overholtzer and Motta 1999; Harborne et al. 2006). Outplanting efforts can create habitat for juvenile fishes which could be beneficial to stoplight parrotfish and other taxa. Herbivore biomass is a known predictor of herbivory rate (Lefcheck et al. 2019), which means that a local rise in the abundance of grazers could drastically reduce algae cover and promote reef recovery by reducing competition and increasing coral recruitment (Mumby et al. 2006b; Hughes et al. 2007; Burkepile and Hay 2008). If outplanting *A. cervicornis* can elicit an increase in the number of algae consumers this would provide further incentive for conducting *A. cervicornis* restoration.

After five years, it appears that outplanting *A. cervicornis* is creating a positive feedback loop in the area of enhanced reef. Overtime, the outplanted colonies are contributing structure to the reef that should be sustained long-term through the live coral tissue. This structure is then creating habitat for reef fishes, and grazers in particular. Those grazers in turn can help the corals through algae removal which can reduce competition and create new settlement area for juvenile corals

Future studies should aim to address whether more than five years is required for outplant sites to attract a greater abundance of larger fishes, piscivores, and commercially important species, or whether these sites will continue to serve as refugia for juvenile and small-bodied adult fishes. These questions could also be answered by outplanting colonies at a larger size.

However, the additional time required to grow larger colonies *in situ* increases the time between outplanting events which is critical to preserving the species and nearshore environments of Southeast Florida and the Caribbean.

In conclusion, this study provides valuable insight into the ecosystem benefits of outplanting *A. cervicornis*. Species recovery may be possible through active restoration efforts, but the increasing threats of climate change, pollutants and excess nutrients, and a declining population of grazers will continue to hinder this process. Reef managers and practitioners alike should strive to increase stony coral cover not only to protect the corals themselves, but also to enhance fish abundance and diversity, which have been linked to greater functional redundancy on coral reefs (Newman et al. 2006; Halpern and Floeter 2008; Rogers et al. 2014; Holbrook et al. 2015; Darling et al. 2017). Outplanting *A. cervicornis* provides the structural complexity required by grazing fishes, while grazers reduce algae competition and promote coral recruitment, creating a positive feedback loop that can benefit the reef community as a whole (Aronson and Precht 2006).

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## References

- Abrams RW, Abrams MD, Schein MW (1983) Diurnal observations on the behavioral ecology of *Gymnothorax moringa* (Cuvier) and *Muraena miliaris* (Kaup) on a Caribbean coral reef. *Coral Reefs* 1:185-192
- Adam TC, Burkepile DE, Ruttenberg BI, Paddock MJ (2015) Herbivory and the resilience of Caribbean coral reefs: knowledge gaps and implications for management. *Mar Ecol Prog Ser* 520:1-20
- Adam TC, Schmitt RJ, Holbrook SJ, Brooks AJ, Edmunds PJ, Carpenter RC (2011) Herbivory, connectivity, and ecosystem resilience: response of a coral reef to a large-scale perturbation. *PLoS One* 6:e23717
- Addis DT, Patterson WF, Dance MA (2007) Site fidelity and movement of reef fishes tagged at unreported artificial reef sites off NW Florida. *Proceedings of the Gulf and Caribbean Fisheries Institute* 60:297-304
- Agudo-Adriani EA, Cappelletto J, Cavada-Blanco F, Croquer A (2016) Colony geometry and structural complexity of the endangered species *Acropora cervicornis* partly explains the structure of their associated fish assemblage. *PeerJ* 4:1-23
- Aguilar-Perera A (2003) Abundance and distribution of hamlets (Teleostei: *Hypoplectrus*) in coral reefs off southwestern Puerto Rico: Support for the multiple-species theory. *Caribb J Sci* 39:147-150
- Allen LG, Bouvier LS, Jenson RE (1992) Abundance, diversity, and seasonality of cryptic fishes and their contribution to a temperate reef fish assemblage off Santa Catalina Island, California. *Bull Southern Calif Acad Sci* 91:55-69
- Allgeier JE, Layman CA, Mumby PJ, Rosemond AD (2014) Consistent nutrient storage and supply mediated by diverse fish communities in coral reef ecosystems. *Glob Chang Biol* 20:2459-2472
- Arena PT, Jordan LKB, Spieler RE (2007) Fish assemblages on sunken vessels and natural reefs in southeast Florida, USA. *Hydrobiologia* 580:157-171
- Aronson RB, Precht WF (2001) White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia* 460:25-38
- Aronson RB, Precht WF (2006) Conservation, precaution, and Caribbean reefs. *Coral Reefs* 25:441-450
- Aronson RB, Bruckner AW, Moore A, Precht WF, Weil E (2008) *Acropora cervicornis*. Version 2013.1:www.iucnredlist.org
- Ault TR, Johnson CR (1998) Spatially and temporally predictable fish communities on coral reefs. *Ecol Monogr* 68:25-50

- Bak RPM, Carpay MJE, de Ruyter van Steveninck ED (1984) Densities of the sea urchin *Diadema antillarum* before and after mass mortalities on the coral reefs of Curaçao. *Mar Ecol Prog Ser* 17:105-108
- Beck MW, Losada IJ, Menendez P, Reguero BG, Diaz-Simal P, Fernandez F (2018) The global flood protection savings provided by coral reefs. *Nat Commun* 9:2186
- Berg R (2013) Tropical cyclone report Hurricane Isaac. In: Center NH (ed) 1-78
- Beukers JS, Jones GP (1997) Habitat complexity modifies the impact of piscivores on a coral reef fish population. *Oecologia* 114:50-59
- Blake ES, Kimberlain TB, Berg R, Cangialosi JP, Beven JL (2013) Tropical cyclone report Hurricane Sandy. In: Center NH (ed) 1-157
- Bohnsack JA (1989) Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bull Mar Sci* 44:631-645
- Brander LM, Rehdanz K, Tol RSJ, H. vBPJ (2012) The economic impact of ocean acidification on coral reefs. *Clim Change Econ* 3
- Brandt ME, Zurcher N, Acosta A, Ault JS, Bohnsack JA, Feeley MW, Harper DE, Hut JH, Kellison T, McClellan DB, Patterson ME, Smith SG (2009) A cooperative multi-agency reef fish monitoring protocol for the Florida Keys coral reef ecosystem Natural Resource Report NPS/SFCN/NRR-2009/150. National Park Service, Fort Collins, Colorado
- Broadman MR, Cummins H (2016) Coral reef fishes: common fish of the Caribbean. Environmental Education and Sustainability, LLC, Oxford, OH
- Brock RE (1982) A critique of the visual census method for assessing coral reef fish populations. *Bull Mar Sci* 32:269-276
- Bruggemann JH, van Oppen MJH, Breeman AM (1994) Foraging by the stoplight parrotfish *Sparisoma viride*. I. Food selection in different, socially determined habitats. *Mar Ecol Prog Ser* 106:41-55
- Burkepile DE, Hay ME (2008) Herbivore species richness and feeding complementarity affect community structure and function on a coral reef. *PNAS* 105:16201-16206
- Burkepile DE, Hay ME (2011) Feeding complementarity versus redundancy among herbivorous fishes on a Caribbean reef. *Coral Reefs* 30:351-362
- Bythell JC, Gladfelter EH, Bythell M (1993) Chronic and catastrophic natural mortality of three common Caribbean reef corals. *Coral Reefs* 12:143-152
- Cabaitan PC, Gomez ED, Aliño PM (2008) Effects of coral transplantation and giant clam restocking on the structure of fish communities on degraded patch reefs. *J Exp Mar Biol Ecol* 357:85-98

- Carpenter KE, Miclat RI, Albaladejo VD, Corpuz VT (1981) The influence of substrate structure on the local abundance and diversity of Philippine reef fishes. Proc 4th Int Coral Reef Symp 2:497-502
- Carpenter RC (1990) Mass mortality of *Diadema antillarum*. II. Effects on population densities and grazing intensity of parrotfishes and surgeonfishes. Mar Biol 104:79-86
- Chittaro PM, Sale PF (2003) Structure of patch-reef fish assemblages at St. Croix, US Virgin Islands, and One Tree Reef, Australia. Mar Ecol Prog Ser 249:277-287
- Colin PL (1973) Burrowing behavior of the yellowhead Jawfish, *Opistognathus aurifrons* Copeia 1973:84-90
- Corless M, Hatcher BG, Hunte W, Scott S (1997) Assessing the potential for fish migration from marine reserves to adjacent fishes areas in Soufriere Marine Management Area. 49th Gulf and Caribbean Fisheries Institute:71-98
- Cramer KL, O'Dea A, Clark TR, Zhao JX, Norris RD (2017) Prehistorical and historical declines in Caribbean coral reef accretion rates driven by loss of parrotfish. Nat Commun 8:14160
- D'Antonio NL, Gilliam DS, Walker BK (2016) Investigating the spatial distribution and effects of nearshore topography on *Acropora cervicornis* abundance in Southeast Florida. PeerJ 4:e2473
- Darling ES, Graham NAJ, Januchowski-Hartley FA, Nash KL, Pratchett MS, Wilson SK (2017) Relationships between structural complexity, coral traits, and reef fish assemblages. Coral Reefs 36:561-575
- Enochs IC, Manzello DP, Carlton R, Schopmeyer S, van Hooidonk R, Lirman D (2014) Effects of light and elevated pCO<sub>2</sub> on the growth and photochemical efficiency of *Acropora cervicornis*. Coral Reefs 33:477-485
- Ferro FB, Jordan LK, Spieler RE (2005) The marine fishes of Broward County, Florida: Final report of 1998-2002 survey results. NOAA Technical Memorandum NMFS-SEFSC-532 78
- Froese R, Pauly D (2018) FishBase, World Wide Web
- Gardner TA, Cote IM, Gill JA, Grant A, Watkinson AR (2005) Hurricanes and Caribbean coral reefs: impacts, recovery patterns, and role in long-term decline. Ecology 86:174-184
- Gilliam DS, Walton CJ, Hayes NK (2016) Southeast Florida Coral Reef Evaluation and Monitoring Project 2016 Year 14 Final Report. Florida DEP Report #RM085, Miami Beach, FL 1-66
- Goergen EA, Gilliam DS (2018) Outplanting technique, host genotype, and site affect the initial success of outplanted *Acropora cervicornis*. PeerJ 6:e4433

- Gratwicke B, Speight MR (2005) The relationship between fish species richness, abundance and habitat complexity in a range of shallow tropical marine habitats. *J Fish Biol* 66:650-667
- Grober-Dunsmore R, Frazer TK, Lindberg WJ, Beets J (2007) Reef fish and habitat relationships in a Caribbean seascape: the importance of reef context. *Coral Reefs* 26:201-216
- Halpern BS, Floeter SR (2008) Functional diversity responses to changing species richness in reef fish communities. *Mar Ecol Prog Ser* 364:147-156
- Harborne AR, Mumby PJ, Micheli F, Perry CT, Dahlgren CP, Holmes KE, Brumbaugh DR (2006) The functional value of Caribbean coral reef, seagrass and mangrove habitats to ecosystem processes. *Adv Mar Biol* 50:57-189
- Herler J, Munday PL, Hernaman V (2011) Gobies on Coral Reefs. In: Patzner RA, Van Tassell JL, Kovačić M, Kapoor BG (eds) *The Biology of Gobies*. Science Publishers, Jersey, British Isles, New Hampshire, pp685
- Hernández-Delgado EA, Mercado-Molina AE, Alejandro-Camis PJ, Candelas-Sánchez F, Fonseca-Miranda JS, González-Ramos CM, Guzmán-Rodríguez R, Mège P, Montañez-Acuña AA, Maldonado IO, Otaño-Cruz A, Suleimán-Ramos SE (2014) Community-based coral reef rehabilitation in a changing climate: lessons learned from hurricanes, extreme rainfall, and changing land use impacts. *Open J Ecol* 04:918-944
- Heron SF, Maynard JA, van Hooidek R, Eakin CM (2016) Warming trends and bleaching stress of the world's coral reefs 1985-2012. *Sci Rep* 6:38402
- Hobson ES (1991) Trophic relationships of fishes specialized to feed on zooplankton above coral reefs In: Sale PF (ed) *The Ecology of Fishes on Coral Reefs*. Academic Press Limited, London, pp69-95
- Hoegh-Guldberg O, Jacob D, Taylor M (2018) Chapter 3: Impacts of 1.5°C global warming on natural and human systems. In: Marengo JA, Pereira J, Sherstyukov B (eds) *Special Report on Global Warming 15°C*. Intergovernmental Panel on Climate Change (IPCC), Incheon, Republic of Korea, pp1-243
- Hogarth WT (2006) Endangered and threatened species: final listing determinations for the elkorn coral and staghorn coral *Fed Register* 71:26852-26872
- Holbrook SJ, Schmitt RJ, Messmer V, Brooks AJ, Srinivasan M, Munday PL, Jones GP (2015) Reef fishes in biodiversity hotspots are at greatest risk from loss of coral species. *PLoS One* 10:e0124054
- Hollarsmith JA, Griffin SP, Moore TD (2012) Success of outplanted *Acropora cervicornis* colonies in reef restoration. *Proc 12th Int Coral Reef Symp*
- Hughes TP (1994) Catastrophes, phase shifts, and large-scale degradation of a Caribbean coral reef. *Science* 256:1547-1551

- Hughes TP, Rodrigues MJ, Bellwood DR, Ceccarelli D, Hoegh-Guldberg O, McCook L, Moltchaniskyj N, Pratchett MS, Steneck RS, Willis B (2007) Phase shifts, herbivory, and the resilience of coral reefs to climate change. *Curr Biol* 17:360-365
- Hughes TP, Barnes ML, Bellwood DR, Cinner JE, Cumming GS, Jackson JBC, Kleypas J, van de Leemput IA, Lough JM, Morrison TH, Palumbi SR, van Nes EH, Scheffer M (2017a) Coral reefs in the Anthropocene. *Nature* 546:82-90
- Hughes TP, Kerry JT, Alvarez-Noriega M, Alvarez-Romero JG, Anderson KD, Baird AH, Babcock RC, Beger M, Bellwood DR, Berkelmans R, Bridge TC, Butler IR, Byrne M, Cantin NE, Comeau S, Connolly SR, Cumming GS, Dalton SJ, Diaz-Pulido G, Eakin CM, Figueira WF, Gilmour JP, Harrison HB, Heron SF, Hoey AS, Hobbs JA, Hoogenboom MO, Kennedy EV, Kuo CY, Lough JM, Lowe RJ, Liu G, McCulloch MT, Malcolm HA, McWilliam MJ, Pandolfi JM, Pears RJ, Pratchett MS, Schoepf V, Simpson T, Skirving WJ, Sommer B, Torda G, Wachenfeld DR, Willis BL, Wilson SK (2017b) Global warming and recurrent mass bleaching of corals. *Nature* 543:373-377
- Humann P (1994) Reef Fish Identification: Florida, Caribbean, Bahamas. New World Pubns Inc.
- Huntington BE, Miller MW, Pausch R, Richter L (2017) Facilitation in Caribbean coral reefs: high densities of staghorn coral foster greater coral condition and reef fish composition. *Oecologia* 184:247-257
- IUCN (2017) Overfishing, reef decline threaten greater Caribbean and Pacific island fisheries. International Union for Conservation of Nature
- IUCN (2018) The IUCN Red List of Threatened Species
- Jaap WC (2000) Coral reef restoration. *Ecol Eng* 15:345-364
- Jaap WC, Sargent FJ (1994) The status of the remnant population of *Acropora palmata* (Lamarck, 1816) at Dry Tortugas National Park, Florida, with a discussion of possible causes of changes since 1881. The Colloquium on Global Aspects of Coral Reefs: Health, Hazards and History:101-105
- Jackson J, Donovan M, Cramer K, Lam V (2014) Status and trends of Caribbean coral reefs: 1970-2012. In: Jeremy Jackson MD, Katie Cramer, Vivian Lam (ed). Global Coral Reef Monitoring Network, IUCN, Gland
- Jackson JB, Kirby MX, Berger WH, Bjorndal KA, Botsford LW, Bourque BJ, Bradbury RH, Cooke R, Erlandson J, Estes JA, Hughes TP, Kidwell S, Lange CB, Leniham HS, Pandolfi JM, Peterson CH, Steneck RS, Tegner MJ, Warner RR (2001) Historical overfishing and the recent collapse of coastal ecosystems. *Science* 293:629-638
- Johnson ME, Lustic C, Bartels E, Baums IB, Gilliam DS, Larson EA, Lirman D, Miller MW, Nedimyer N, Shopmeyer S (2011) Caribbean *Acropora* restoration guide: best practices for propagation and population enhancement. The Nature Conservancy, Arlington, VA 1-64

- Jones GP, McCormick MI, Srinivasan M, Eagle JV, Paine RT (2004) Coral declines threatens fish biodiversity in marine reserves. *PNAS* 101:8251-8253
- Jordan-Dahlgreen E, Rodriguez-Martinez RE (1998) Post-hurricane initial recovery of *Acropora palmata* in two reefs of the Yucatan Peninsula, Mexico. *Bull Mar Sci* 63:213-228
- Kiel C, Huntington BE, Miller MW (2012) Tractable field metrics for restoration and recovery monitoring of staghorn coral *Acropora cervicornis*. *Endangered Species Research* 19:171-176
- Kilfoyle K, Fisco DP, Smith SG, Spieler RE (2015) Southeast Florida coral reef fishery-independent baseline assessment--2012-2014 summary report Florida Department of Environmental Protection 1-129
- Knowlton N, Lang JC, Keller BD (1990) Case study of natural population collapse: post-hurricane predation on Jamaican staghorn corals. *Smithsonian Contributions to Marine Science* 31:1-25
- Lefcheck JS, Innes-Gold AA, Brandl SJ, Steneck RS, Torres RE, Rasher DB (2019) Tropical fish diversity enhances coral reef functioning across multiple scales. *Sci Adv* 5:1-7
- Lemoine NP, Valentine JF (2012) Structurally complex habitats provided by *Acropora palmata* influence ecosystem processes on a reef in the Florida Keys National Marine Sanctuary. *Coral Reefs* 31:779-786
- Lessios HA (1988) Mass mortality of *Diadema antillarum* in the Caribbean: what have we learned? *Ann Rev Ecol Syst* 19:371-393
- Lessios HA, Robertson DR, Cubit JD (1984) Spread of *Diadema* mass mortality through the Caribbean. *Science* 226:335-337
- Lirman D (1999) Reef fish communities associated with *Acropora palmata*: relationships to benthic attributes. *Bull Mar Sci* 65:235-252
- Lirman D, Fong P (1997) Patterns of damage to the branching coral *Acropora palmata* following Hurricane Andrew: damage and survivorship of hurricane-generated asexual recruits. *J Coastal Res* 13:67-72
- Lirman D, Bowden-kerby A, Schopmeyer S, Huntington B, Thyberg T, Gough M, Gough T, Gough R, Gough Y (2010) A window to the past: Documenting the status of one of the last remaining 'megapopulations' of the threatened staghorn coral *Acropora cervicornis* in the Dominican Republic. *Aquat Conserv* 20:773-781
- Lucas MQ, Weil E (2015) Recent recovery in *Acropora cervicornis* and abundance of *A. prolifera* off La Parguera, Puerto Rico. *Marine Biodiversity* 46:531-532
- Luckhurst BE, Luckhurst K (1977) Recruitment patterns of coral reef fishes on the fringing reefs of Curaçao, Netherlands Antilles. *Can J Zool* 55:681-689

- Luckhurst BE, Luckhurst K (1978) Analysis of the influence of substrate variables on coral reef fish communities. *Mar Biol* 49:317-323
- McDougall PT, Kramer DL (2006) Short-term behavioral consequences of territory relocation in a Caribbean damselfish, *Stegastes diencaeus*. *Behav Ecol* 18:53-61
- McEachran JD, Fechhelm JD (eds) (2005) *Fishes of the Gulf of Mexico*. University of Texas Press, Austin
- Mercado-Molina AE, Ruiz-Diaz CP, Pérez ME, Rodríguez-Barreras R, Sabat AM (2015) Demography of the threatened coral *Acropora cervicornis*: implications for its management and conservation. *Coral Reefs* 34:1113-1124
- Miller MW, Bourque AS, Bohnsack JA (2002) An analysis of the loss of Acroporid corals at Looe Key, Florida, USA: 1983–2000. *Coral Reefs* 21:179-182
- Moyer RP, Riegl B, Banks K, Dodge RE (2003) Spatial patterns and ecology of benthic communities on a high-latitude South Florida (Broward County, USA) reef system. *Coral Reefs* 22:447-464
- Mumby PJ, Hedley JD, Zychaluk K, Harborne AR, Blackwell PG (2006a) Revisiting the catastrophic die-off of the urchin *Diadema antillarum* on Caribbean coral reefs: fresh insights on resilience from a simulation model. *Ecological Modelling* 196:131-148
- Mumby PJ, Dahlgren CP, Harborne AR, Kappel CV, Micheli F, Brumbaugh DR, Holmes KE, Mendes JM, Broad K, Sanchirico JN, Buch K, Box S, Stoffle RW, Gill AB (2006b) Fishing, trophic cascades, and the process of grazing on coral reefs. *Science* 311:98-101
- Munro JL, Gaut VC, Thompson R, Reeson PH (1973) The spawning seasons of Caribbean reef fishes. *J Fish Biol* 5:69-84
- Nedimyer N, Gaines K, Roach S (2011) Coral tree nursery: An innovative approach to growing corals in an ocean-based field nursery. *AAACL Bioflux* 4:442-446
- Nemeth M, Griffin S, Moore T, Meehan S (2016) The structure of fish assemblages on restored and un-restored coral reef habitats impacted by ship groundings
- Nemtsov SC (1997) Intraspecific variation in home range exclusivity by female green razorfish, *Xyrichtys splendens* (family Labridae), in different habitats. *Environ Biol Fish* 50:371-381
- Newman MJ, Paredes GA, Sala E, Jackson JB (2006) Structure of Caribbean coral reef communities across a large gradient of fish biomass. *Ecol Lett* 9:1216-1227
- O'Rourke A, Kremb S, Bader TM, Helfer M, Schmitt-Kopplin P, Gerwick WH, Brack-Werner R, Voolstra CR (2016) Alkaloids from the sponge *Stylissa carteri* present prospective scaffolds for the inhibition of Human Immunodeficiency Virus 1 (HIV-1). *Mar Drugs* 14:1-10

- Ogden JC, Buckman NS (1973) Movements, foraging groups, and diurnal migrations of the striped parrotfish *Scarus croicensis* Bloch (Scaridae). *Ecology* 54:589-596
- Ogden JC, Ehrlich PR (1977) The behavior of heterotypic resting schools of juvenile grunts (Pomadasyidae). *Mar Biol* 42:273-280
- Omori M, Iwao K (2014) Methods of farming sexually propagated corals and outplanting for coral reef rehabilitation; with list of references for coral reef rehabilitation through active restoration measure. Akajima Marine Science Laboratory Okinawa, Japan 1-63
- Opel AH, Cavanaugh CM, Rotjan RD, Nelson JP (2017) The effect of coral restoration on Caribbean reef fish communities. *Mar Biol* 164:1-16
- Overholtzer KL, Motta PJ (1999) Comparative resource use by juvenile parrotfishes in the Florida Keys. *Mar Ecol Prog Ser* 177:177-187
- Paddack MJ, Reynolds JD, Aguilar C, Appeldoorn RS, Beets J, Burkett EW, Chittaro PM, Clarke K, Esteves R, Fonseca AC, Forrester GE, Friedlander AM, Garcia-Sais J, Gonzalez-Sanson G, Jordan LK, McClellan DB, Miller MW, Molloy PP, Mumby PJ, Nagelkerken I, Nemeth M, Navas-Camacho R, Pitt J, Polunin NV, Reyes-Nivia MC, Robertson DR, Rodriguez-Ramirez A, Salas E, Smith SR, Spieler RE, Steele MA, Williams ID, Wormald CL, Watkinson AR, Cote IM (2009) Recent region-wide declines in Caribbean reef fish abundance. *Curr Biol* 19:590-595
- Parris R (2016) *Halichoeres poeyi* (blackear wrasse) The Online Guide to the Animals of Trinidad and Tobago. University of the West Indies
- Pascal N, Allenbach M, Brathwaite A, Burke L, Le Port G, Clua E (2016) Economic valuation of coral reef ecosystem service of coastal protection: a pragmatic approach. *Ecosyst Serv* 21:72-80
- Patzner RA, Gonçalves EJ, Hastings PA, Kapoor BG (eds) (2009) *The Biology of Blennies*. CRC Press, Boca Raton, FL
- Pratchett MS, Wilson SK, Munday PL (2015) Effects of climate change on coral reef fishes. In: Mora C (ed) *Ecology of fishes on coral reefs*. Cambridge University Press, Cambridge, pp127-134
- Precht WF, Bruckner AW, Aronson RB, Bruckner RJ (2002) Endangered Acroporid Corals of the Caribbean. *Coral Reefs* 21:41-42
- Precht WF, Aronson RB, Moody RM, Kaufman L (2010) Changing patterns of microhabitat utilization by the threespot damselfish, *Stegastes planifrons*, on Caribbean reefs. *PLoS One* 5:e10835
- Pressley PH (1980) Lunar periodicity in the spawnin of yellowtail damselfish, *Microspathodon chrysurus*. *Environ Biol Fish* 5:153-159

- Quinn NJ, Kojis BL (2007) Evaluating artificial means to increase *Acropora* coral populations and increase associated fish communities in Jamaica. 58th Gulf and Caribbean Fisheries Institute:29-34
- R Core Team (2016) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria
- Roberts CM, Ormond RFG (1987) Habitat complexity and coral reef diversity and abundance on Red Sea fringing reefs. *Mar Ecol Prog Ser* 40:1-8
- Robertson DR, Van Tassell JL (2015) Shorefishes of the greater Caribbean: online information system. Smithsonian Tropical Research Institute Version 10
- Rogers A, Blanchard JL, Mumby PJ (2014) Vulnerability of coral reef fisheries to a loss of structural complexity. *Curr Biol* 24:1000-1005
- Rogers CS, Suchanek TH, Pecora FA (1982) Effects of hurricanes David and Frederic (1979) on shallow *Acropora palmata* reef communities: St. Croix, U.S. Virgin Islands. *Bull Mar Sci* 32:532-548
- Schopmeyer SA, Lirman D, Bartels E, Gilliam DS, Goergen EA, Griffin SP, Johnson ME, Lusic C, Maxwell K, Walter CS (2017) Regional restoration benchmarks for *Acropora cervicornis*. *Coral Reefs* 36:1047-1057
- Shaish L, Levy G, Katzir G, Rinkevich B (2010) Employing a highly fragmented, weedy coral species in reef restoration. *Ecol Eng* 36:1424-1432
- Spalding M, Burke L, Wood SA, Ashpole J, Hutchison J, zu Ermgassen P (2017) Mapping the global value and distribution of coral reef tourism. *Mar Policy* 82:104-113
- Sponaugle S, Cowen RK (1996) Larval supply and patterns of recruitment for two Caribbean reef fishes, *Stegastes partitus* and *Acanthurus bahianus*. *Mar Freshwater Res* 47:433-447
- Sponaugle S, Cowen RK (1997) Early life history traits and recruitment patterns of Caribbean wrasses (Labridae). *Ecol Monogr* 67:177-202
- Steneck RS (1994) Is herbivore loss more damaging to reefs than hurricanes? Case studies from two Caribbean reef systems (1978-1988). *Colloquium on Global Aspect of Coral Reefs: Health, Hazards and History*:220-226
- Tolimieri N (1998) Effects of substrata, resident conspecifics and damselfish on the settlement and recruitment of the stoplight parrotfish, *Sparisoma viride*. *Environ Biol Fish* 53:393-404
- van Woesik R, Ripple K, Miller SL (2018) Macroalgae reduces survival of nursery-reared *Acropora* corals in the Florida reef tract. *Restor Ecol* 26:563-569

- Vargas-Angel B, Thomas JD, Hoke SM (2003) High-latitude *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. *Coral Reefs* 22:465-473
- Walker BK, Riegl B, Dodge RE (2008) Mapping coral reef habitats in southeast Florida using a combined technique approach. *J Coastal Res* 245:1138-1150
- Walker BK, Jordan LKB, Spieler RE (2009) Relationship of reef fish assemblages and topographic complexity on southeastern Florida coral reef habitats. *J Coastal Res* 10053:39-48
- Walker BK, Larson EA, Moulding AL, Gilliam DS (2012) Small-scale mapping of indeterminate arborescent Acroporid coral (*Acropora cervicornis*) patches. *Coral Reefs* 31:885-894
- Warner R, Robertson D, Leigh E (1975) Sex change and sexual selection. *Science* 190:633-638
- Wilkes AA, Cook MM, DiGirolamo AL, Eme J, Grim JM, Hohmann BC, Conner SL, McGill CJ, Pomory CM, Bennett WA (2008) A comparison of damselfish densities on live staghorn coral (*Acropora cervicornis*) and coral rubble in Dry Tortugas National Park. *Southeast Nat* 7:483-492
- Woodley JD, Chornesky EA, Clifford PA, Jackson JBC, Kaufman LS, Knowlton N, Lang JC, Pearson MP, Porter JW, Rooney MC, Rylaarsdam KW, Tunnicliffe VJ, Wahle CM, Wulff JL, Curtis ASG, Dallmeyer MD, Jupp BP, Koel MAR, Neigel J, Sides EM (1981) Hurricane Allen's impact on Jamaican coral reefs. *Science* 214:749-755
- Yap HT (2009) Local changes in community diversity after coral transplantation. *Mar Ecol Prog Ser* 374:33-41
- Young CN, Schopmeyer SA, 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
- Zaneveld JR, Burkepile DE, Shantz AA, Pritchard CE, McMinds R, Payet JP, Welsh R, Correa AM, Lemoine NP, Rosales S, Fuchs C, Maynard JA, Thurber RV (2016) Overfishing and nutrient pollution interact with temperature to disrupt coral reefs down to microbial scales. *Nat Commun* 7:11833

## Appendices

Appendix 1. All observed species listed alphabetically by family name. \*Indicates species that were removed for all richness calculations.

|   | <b>Species Name</b>                | <b>Common Name</b>   | <b>Family</b>  | <b>Functional Group</b> | <b>Location</b>   | <b>Source</b>            |
|---|------------------------------------|----------------------|----------------|-------------------------|-------------------|--------------------------|
|   | <i>Acanthurus coeruleus</i>        | Blue tang            | Acanthuridae   | Herbivore               | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Acanthurus chirurgus</i>        | Doctorfish           | Acanthuridae   | Herbivore               | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Acanthurus bahianus</i>         | Ocean surgeonfish    | Acanthuridae   | Herbivore               | Outplant, Control | (Burkepile and Hay 2008) |
| * | Blenniidae spp.                    | Blenny spp.          | Blenniidae     | Microinvertivore        | Outplant, Control | (Patzner et al. 2009)    |
|   | <i>Ophioblennius macclurei</i>     | Redlip blenny        | Blenniidae     | Herbivore               | Control           | (IUCN 2018)              |
|   | <i>Parablennius marmoratus</i>     | Seaweed blenny       | Blenniidae     | Omnivore                | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Acanthemblemaria aspera</i>     | Roughhead blenny     | Chaenopsidae   | Microinvertivore        | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Emblemaria pandionis</i>        | Sailfin blenny       | Chaenopsidae   | Microinvertivore        | Outplant, Control | (Patzner et al. 2009)    |
|   | <i>Acanthemblemaria spinosa</i>    | Spinyhead blenny     | Chaenopsidae   | Planktivore             | Outplant          | (Froese and Pauly 2018)  |
|   | <i>Chaetodon capistratus</i>       | Fourey butterflyfish | Chaetodontidae | Macroinvertivore        | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Diodon holocanthus</i>          | Balloonfish          | Diodontidae    | Macroinvertivore        | Outplant          | (Froese and Pauly 2018)  |
|   | <i>Coryphopterus glaucofraenum</i> | Bridled goby         | Gobiidae       | Microinvertivore        | Outplant, Control | (IUCN 2018)              |
|   | <i>Coryphopterus cirratus</i>      | Colon goby           | Gobiidae       | Microinvertivore        | Outplant, Control | (IUCN 2018)              |
|   | <i>Gnatholepis thompsoni</i>       | Goldspot goby        | Gobiidae       | Microinvertivore        | Outplant, Control | (Herler et al. 2011)     |
|   | <i>Coryphopterus personatus</i>    | Masked goby          | Gobiidae       | Planktivore             | Control           | (IUCN 2018)              |
|   | <i>Elacatinus oceanops</i>         | Neon goby            | Gobiidae       | Microinvertivore        | Outplant, Control | (Humann 1994)            |
|   | <i>Anisotremus surinamensis</i>    | Black margate        | Haemulidae     | Piscivore-invertivore   | Control           | (Froese and Pauly 2018)  |
|   | <i>Haemulon flavolineatum</i>      | French grunt         | Haemulidae     | Macroinvertivore        | Outplant, Control | (Froese and Pauly 2018)  |
| * | <i>Haemulon</i> spp.               | Juvenile grunts      | Haemulidae     | Macroinvertivore        | Outplant, Control | (Ogden and Ehrlich 1977) |
|   | <i>Haemulon aurolineatum</i>       | Tomtate              | Haemulidae     | Omnivore                | Outplant          | (Froese and Pauly 2018)  |
|   | <i>Haemulon plumierii</i>          | White grunt          | Haemulidae     | Piscivore-invertivore   | Outplant, Control | (Froese and Pauly 2018)  |
|   | <i>Halichoeres poeyi</i>           | Blackear wrasse      | Labridae       | Macroinvertivore        | Outplant, Control | (Parris 2016)            |
|   | <i>Thalassoma bifasciatum</i>      | Bluehead             | Labridae       | Planktivore             | Outplant, Control | (Froese and Pauly 2018)  |

|  | <b>Species Name</b>               | <b>Common Name</b>     | <b>Family</b>   | <b>Functional Group</b> | <b>Location</b>   | <b>Source</b>                                |
|--|-----------------------------------|------------------------|-----------------|-------------------------|-------------------|--|
|  | <i>Halichoeres maculipinna</i>    | Clown wrasse           | Labridae        | Piscivore-invertivore   | Outplant, Control | (McEachran and Fehhelm 2005)                 |
|  | <i>Clepticus parrae</i>           | Creole wrasse          | Labridae        | Planktivore             | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Xyrichtys splendens</i>        | Green razorfish        | Labridae        | Planktivore             | Outplant          | (Nemtsov 1997)                               |
|  | <i>Halichoeres caudalis</i>       | Painted wrasse         | Labridae        | Piscivore-invertivore   | Outplant          | (Robertson and Van Tassell 2015)             |
|  | <i>Halichoeres radiatus</i>       | Puddingwife            | Labridae        | Macroinvertivore        | Outplant, Control | (Froese and Pauly 2018)                      |
|  | <i>Halichoeres bivittatus</i>     | Slippery dick          | Labridae        | Piscivore-invertivore   | Outplant, Control | (Froese and Pauly 2018)                      |
|  | <i>Halichoeres garnoti</i>        | Yellowhead wrasse      | Labridae        | Microinvertivore        | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Paraclinus fasciatus</i>       | Banded blenny          | Labrisomidae    | Microinvertivore        | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Malacoctenus boelkei</i>       | Diamond blenny         | Labrisomidae    | Microinvertivore        | Outplant          | (Patzner et al. 2009)                        |
|  | <i>Labrisomus kalisheriae</i>     | Downy blenny           | Labrisomidae    | Microinvertivore        | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Malacoctenus gilli</i>         | Dusky blenny           | Labrisomidae    | Microinvertivore        | Outplant          | (Patzner et al. 2009)                        |
|  | <i>Labrisomus nuchipinnis</i>     | Hairy blenny           | Labrisomidae    | Macroinvertivore        | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Gobioclinus gobio</i>          | Palehead blenny        | Labrisomidae    | Microinvertivore        | Control           | (Patzner et al. 2009; Froese and Pauly 2018) |
|  | <i>Malacoctenus macropus</i>      | Rosy blenny            | Labrisomidae    | Microinvertivore        | Outplant, Control | (Patzner et al. 2009)                        |
|  | <i>Malacoctenus triangulatus</i>  | Saddled blenny         | Labrisomidae    | Microinvertivore        | Outplant, Control | (Froese and Pauly 2018)                      |
|  | <i>Lutjanus synagris</i>          | Lane snapper           | Lutjanidae      | Piscivore-invertivore   | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Ocyurus chrysurus</i>          | Yellowtail snapper     | Lutjanidae      | Piscivore-invertivore   | Outplant, Control | (Froese and Pauly 2018)                      |
|  | <i>Monacanthus ciliatus</i>       | Fringed filefish       | Monacanthidae   | Omnivore                | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Cantherhines pullus</i>        | Orangespotted filefish | Monacanthidae   | Microinvertivore        | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Monacanthus tuckeri</i>        | Slender filefish       | Monacanthidae   | Omnivore                | Outplant          | (Froese and Pauly 2018)                      |
|  | <i>Pseudopeneus maculatus</i>     | Spotted goatfish       | Mullidae        | Macroinvertivore        | Outplant, Control | (Froese and Pauly 2018)                      |
|  | <i>Gymnothorax miliaris</i>       | Goldentail moray       | Muraenidae      | Piscivore-invertivore   | Control           | (Abrams et al. 1983)                         |
|  | <i>Myrichthys breviceps</i>       | Sharptail eel          | Ophichthidae    | Piscivore-invertivore   | Outplant          | (IUCN 2018)                                  |
|  | <i>Opistognathus macrognathus</i> | Banded jawfish         | Opistognathidae | Piscivore-invertivore   | Outplant          | (Froese and Pauly 2018)                      |

|   | <b>Species Name</b>            | <b>Common Name</b>     | <b>Family</b>   | <b>Functional Group</b> | <b>Location</b>   | <b>Source</b>               |
|---|--------------------------------|------------------------|-----------------|-------------------------|-------------------|-----------------------------|
|   | <i>Opistognathus aurifrons</i> | Yellowhead jawfish     | Opistognathidae | Planktivore             | Outplant          | (Colin 1973)                |
|   | <i>Lactophrys triqueter</i>    | Smooth trunkfish       | Ostraciidae     | Macroinvertivore        | Outplant          | (Froese and Pauly 2018)     |
|   | <i>Holacanthus bermudensis</i> | Blue angelfish         | Pomacanthidae   | Macroinvertivore        | Outplant          | (Froese and Pauly 2018)     |
|   | <i>Pomacanthus paru</i>        | French angelfish       | Pomacanthidae   | Omnivore                | Outplant          | (Froese and Pauly 2018)     |
|   | <i>Holocanthus ciliaris</i>    | Queen angelfish        | Pomacanthidae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Holacanthus tricolor</i>    | Rock beauty            | Pomacanthidae   | Omnivore                | Outplant          | (Froese and Pauly 2018)     |
|   | <i>Stegastes leucostictus</i>  | Beaugregory            | Pomacentridae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Stegastes partitus</i>      | Bicolor damselfish     | Pomacentridae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Stegastes variabilis</i>    | Cocoa damselfish       | Pomacentridae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Stegastes adustus</i>       | Dusky damselfish       | Pomacentridae   | Herbivore               | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Stegastes diencaeus</i>     | Longfin damselfish     | Pomacentridae   | Omnivore                | Outplant, Control | (McDougall and Kramer 2006) |
|   | <i>Abudefduf saxatilis</i>     | Sergeant major         | Pomacentridae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Stegastes planifrons</i>    | Threespot damselfish   | Pomacentridae   | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Sparisoma radians</i>       | Bucktooth parrotfish   | Scaridae        | Herbivore               | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Sparisoma atomarium</i>     | Greenblotch parrotfish | Scaridae        | Herbivore               | Outplant          | (Parris 2016)               |
| * | <i>Scarus spp.</i>             | Parrotfish spp.        | Scaridae        | Herbivore               | Outplant          | (Burkepile and Hay 2011)    |
|   | <i>Scarus taeniopterus</i>     | Princess parrotfish    | Scaridae        | Herbivore               | Outplant, Control | (Burkepile and Hay 2008)    |
|   | <i>Scarus vetula</i>           | Queen parrotfish       | Scaridae        | Herbivore               | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Sparisoma aurofrenatum</i>  | Redband parrotfish     | Scaridae        | Herbivore               | Outplant, Control | (Burkepile and Hay 2008)    |
|   | <i>Sparisoma rubripinne</i>    | Redfin parrotfish      | Scaridae        | Herbivore               | Outplant          | (IUCN 2018)                 |
|   | <i>Sparisoma viride</i>        | Stoplight parrotfish   | Scaridae        | Omnivore                | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Scarus iseri</i>            | Striped parrotfish     | Scaridae        | Herbivore               | Outplant, Control | (Froese and Pauly 2018)     |
|   | <i>Pareques acuminatus</i>     | Highhat                | Sciaenidae      | Macroinvertivore        | Outplant, Control | (IUCN 2018)                 |
|   | <i>Equetus punctatus</i>       | Spotted drum           | Sciaenidae      | Macroinvertivore        | Outplant          | (Froese and Pauly 2018)     |

|  | <b>Species Name</b>            | <b>Common Name</b> | <b>Family</b>  | <b>Functional Group</b> | <b>Location</b>   | <b>Source</b>           |
|--|--------------------------------|--------------------|----------------|-------------------------|-------------------|-------------------------|
|  | <i>Hypoplecturus unicolor</i>  | Butter hamlet      | Serranidae     | Piscivore-invertivore   | Outplant          | (Aguilar-Perera 2003)   |
|  | <i>Serranus baldwini</i>       | Lantern bass       | Serranidae     | Piscivore-invertivore   | Outplant, Control | (Froese and Pauly 2018) |
|  | <i>Mycteroperca phenax</i>     | Scamp              | Serranidae     | Piscivore               | Control           | (IUCN 2018)             |
|  | <i>Sphoeroides spengleri</i>   | Bandtail puffer    | Tetraodontidae | Macroinvertivore        | Outplant          | (Froese and Pauly 2018) |
|  | <i>Sphoeroides testudineus</i> | Checkered puffer   | Tetraodontidae | Macroinvertivore        | Outplant          | (Froese and Pauly 2018) |
|  | <i>Canthigaster rostrata</i>   | Sharpnose puffer   | Tetraodontidae | Omnivore                | Outplant, Control | (Froese and Pauly 2018) |
|  | <i>Urobatis jamaicensis</i>    | Yellow stingray    | Urolophidae    | Piscivore-invertivore   | Outplant          | (Froese and Pauly 2018) |

Appendix 2. Regression models of outplant and control sites over time for: overall mean fish abundance, mean species richness, all five size classes, mean grazer abundance and all five size classes of grazers. Significant p-values are bolded.

| Abundance and richness | Outplant |                   |                         | Control |                  |                         |
|------------------------|----------|-------------------|-------------------------|---------|------------------|-------------------------|
|                        | Test     | P                 | R <sup>2</sup> adjusted | Test    | P                | R <sup>2</sup> adjusted |
| Abundance              | GAM      | <b>0.00151</b>    | 0.24                    | GAM     | <b>0.00695</b>   | 0.92                    |
| Species Richness       | GAM      | <b>0.00000101</b> | 0.109                   | GAM     | <b>0.0000622</b> | 0.283                   |
| <2 cm                  | GAM      | <b>0.03</b>       | 0.64                    | GAM     | <b>0.0244</b>    | 0.96                    |
| 2-5 cm                 | GAM      | <b>0.00157</b>    | 0.27                    | GAM     | <b>0.00825</b>   | 0.91                    |
| 5-10 cm                | GAM      | <b>0.00892</b>    | -0.16                   | GAM     | <b>0.0087</b>    | 0.55                    |
| 10-20 cm               | GAM      | 0.07              | 0.87                    | GAM     | 0.13             | 0.09                    |
| 20-50 cm               | GAM      | 0.07              | 0.97                    | GAM     | 0.27             | -0.09                   |
| Grazer Total           | GAM      | <b>0.00754</b>    | 0.87                    | GAM     | <b>0.00355</b>   | -0.01                   |
| Grazer <2 cm           | GAM      | <b>0.0379</b>     | 0.04                    | GAM     | <b>0.03</b>      | -0.25                   |
| Grazer 2-5 cm          | GAM      | <b>0.00405</b>    | 0.99                    | GAM     | <b>0.01</b>      | -0.12                   |
| Grazer 5-10 cm         | GAM      | <b>0.02</b>       | -0.01                   | GAM     | <b>0.00778</b>   | 0.99                    |
| Grazer 10-20 cm        | GAM      | 0.08              | 0.94                    | GAM     | 0.11             | 0.94                    |
| Grazer 20-50 cm        | GAM      | 0.10              | 0.95                    | GAM     | 0.42             | -0.23                   |

Appendix 3. Comparison of outplant and control sites over time for: overall mean fish abundance, mean species richness, all five size classes, mean grazer abundance, and all five size classes of grazers. Significant p-values are bolded.

| Abundance and richness | Test | P              | R <sup>2</sup> adjusted |
|------------------------|------|----------------|-------------------------|
| Abundance              | GAM  | <b>0.0402</b>  | 0.64                    |
| Species Richness       | GAM  | <b>0.0319</b>  | 0.39                    |
| <2 cm                  | GAM  | 0.563          | 0.78                    |
| 2-5 cm                 | GAM  | 0.423          | 0.22                    |
| 5-10 cm                | GAM  | <b>0.00685</b> | 0.71                    |
| 10-20 cm               | GAM  | <b>0.0412</b>  | 0.78                    |
| 20-50 cm               | GAM  | 0.932          | 0.16                    |
| Grazer Total           | GAM  | 0.0723         | 0.40                    |
| Grazer <2 cm           | GAM  | 0.914          | 0.66                    |
| Grazer 2-5 cm          | GAM  | 0.402          | 0.01                    |
| Grazer 5-10 cm         | GAM  | <b>0.00332</b> | 0.83                    |
| Grazer 10-20 cm        | GAM  | <b>0.01651</b> | 0.86                    |
| Grazer 20-50 cm        | GAM  | 0.866          | 0.20                    |

Appendix 4. Regression models of structural complexity (TLE, cm m<sup>-2</sup>) and fish abundance (no. m<sup>-2</sup>) in 2016 for: total fish abundance, species richness, all five size classes, total grazer abundance, and all five size classes of grazers. Significant p-values are bolded.

| Abundance and richness | Test        | P                  | R <sup>2</sup> adjusted |
|------------------------|-------------|--------------------|-------------------------|
| Abundance              | GAM         | <b>0.000000863</b> | 0.72                    |
| Species Richness       | GAM         | <b>0.00000649</b>  | 0.05                    |
| <2 cm                  | GAM         | <b>0.0393</b>      | 0.03                    |
| 2-5 cm                 | GAM         | <b>0.00000619</b>  | 0.53                    |
| 5-10 cm                | GAM         | <b>0.00676</b>     | 0.29                    |
| 10-20 cm               | GAM         | 0.351              | -0.04                   |
| 20-50 cm               | NA          | NA                 | NA                      |
| Grazer Total           | Exponential | <b>0.00276</b>     | NA                      |
| Grazer <2 cm           | GAM         | <b>0.0462</b>      | 0.08                    |
| Grazer 2-5 cm          | Exponential | <b>0.0119</b>      | NA                      |
| Grazer 5-10 cm         | Exponential | <b>0.0163</b>      | NA                      |
| Grazer 10-20 cm        | GAM         | 0.351              | -0.04                   |
| Grazer 20-50 cm        | NA          | NA                 | NA                      |