

Reef-scale trends in Florida *Acropora* spp. abundance and the effects of population
enhancement

Miller MW^{1*}, Kerr KA², Williams DE^{1,2}

1. NOAA National Marine Fisheries Service, Southeast Fisheries Science Center, 75 Virginia Beach Dr. Miami FL 33140 USA

2. Cooperative Institute for Marine and Atmospheric Science, Rosenstiel School of Marine and Atmospheric Science, University of Miami, 4600 Rickenbacker Cswy. Miami FL 33149 USA

*Corresponding Author: Margaret.w.miller@noaa.gov

Keywords: Florida Keys, *Acropora palmata*, *Acropora cervicornis*, GIS, spatial analysis, bleaching, coral nursery, outplanting

Comment [A1]: This study is interesting and addresses some very important questions, including some that proponents of nurseries and outplanting often ignore. Please see my detailed comments inserted below. I have a few other general comments----There should be discussion of how much confidence we can have that the reported benefits result from the outplantings and not from other factors. There is no way for the reader to visualize the outplants—their distribution on the reefs that were compared over the years, their fate (survival, presence of disease, etc.). Was there ever any tracking of individual outplants that can be brought into the discussion here? The Discussion section should include reference to studies in Florida and elsewhere of natural recovery (or lack of recovery) of both of these species. I had trouble following just how the area of thickets was handled. And were there thickets of *A. cervicornis*???

ABSTRACT: Since the listing of *Acropora palmata* and *A. cervicornis* under the U.S. Endangered Species Act in 2006, increasing investments have been made in propagating both species in offshore coral nurseries and outplanting cultured fragments to reef habitats. This investment is superimposed over a spatiotemporal patchwork of ongoing disturbances [such as -----](#) and the potential for natural population recovery. In 2014 and 2015, we repeated broad scale, low resolution *Acropora* spp. [censuses](#) conducted in appropriate reef habitats during 2005-2007 to evaluate the trajectory of local populations and the effect of population enhancement. [Generally](#), *A. palmata* has been the target of much less enhancement effort and has shown small, but often negative changes in reef scale [density](#). Meanwhile, *A. cervicornis* showed a significant increase in colony density at sites where population enhancement had been conducted between 2005 and 2014, with stable or slightly negative trends at sites without population enhancement and a significant correlation of change [increases???](#) in colony density with cumulative numbers of prior outplants across [sites](#). Both enhanced and unenhanced sites showed negative trends for both species between 2014 and [2015](#), reflecting widespread mortality caused by severe thermal bleaching in fall 2014. This study documents a substantive benefit of *Acropora* spp. population enhancement in the Florida Keys against a backdrop of ongoing population [decline](#).

Comment [A2]: What exactly do these censuses include—belongs in Abstract

Comment [A3]: Provide an estimate of the spatial scale over which these censuses were done—the total area involved

Comment [A4]: Not sure what you mean by “negative changes in reef scale density”?? after outplanting fragments there was a net decrease in number of colonies???

Comment [A5]: This statement not clear

Comment [A6]: But you don’t say here whether there were overall net gains in both species in 2015 since 2007—you just say “negative trends”—important to include this

Comment [A7]: Benefits only if enhanced sites had higher densities than unenhanced sites over the time period of interest --- and this wasn’t true for *A. palmata* according to previous statements--- Do you have data on survival of outplants vs naturally occurring colonies?????

INTRODUCTION:

Caribbean coral reefs are home to two species of fast-growing, habitat-forming species of *Acropora* spp. corals; staghorn (*A. cervicornis*) and elkhorn (*A. palmata*). Both are listed as Critically Endangered by IUCN and threatened under the US Endangered Species Act (ESA). Their endangered status accrues from a litany of factors which have caused extensive mortality combined with inadequate recruitment to sustain populations throughout their range. ESA listing carries a legal mandate to ‘recover’ imperiled species. The Acropora Recovery Plan describes [the](#) need for ongoing monitoring and evaluation to track the status of populations, as well as the need to curb ongoing threats ~~related to mortality~~ [\(such as disease and thermal stress due to global climate change\)](#) and proactive population enhancement measures [to](#) jumpstart population recovery (NMFS 2015). Substantial effort has built in [implementing](#) population enhancement throughout the Caribbean (Young et al. 2012), largely following the ‘coral gardening’ model (Epstein et al. 2003; Rinkevich 2015). As the *Acropora* population enhancement effort has grown, substantial management and planning effort has gone to foster pursuit of risk-averse [strategies](#). These strategies include de-emphasis of land-based culture and dispersing individual nursery operations to minimize the geographic [envelope](#) from which source stocks are drawn and propagated fragments are outplanted, and maximizing and tracking the genotypic diversity of cultured [stocks](#). *Acropora* spp. fragments are propagated via fragmentation [of colonies collected where originally??](#) in offshore field nurseries, grown to a viable [\(explain\)](#) size and then outplanted to reef habitats with the goal of re-creating sustainable population patches which can serve as larval sources to jumpstart population recovery on a broader scale (Johnson et al. 2011).

Comment [A8]: Revision needed—words missing?

Comment [A9]: Please be more specific here --- reads like jargon

Comment [A10]: What does de-emphasis of land-based culture mean?

Comment [A11]: What is meant by “geographic envelope”??

Comment [A12]: We also need more information on the susceptibility of different genotypes to thermal stress and diseases

Unfortunately, ~~the fact remains that~~ cultured *Acropora* fragments often behave like their wild counterparts in Caribbean reef communities. ~~This means that~~ they are subject to ongoing chronic and acute stressors, often manifesting substantial mortality in the same pattern as the background population (Miller et al. 2014; Schopmeyer & Lirman 2015). Critics of population enhancement maintain that potentially high levels of mortality would preclude any long term benefit to population recovery, and that the level of investment implies that the scale of effect (e.g., area of reef) will remain **trivial**. Substantial published work has documented the ~~staggering~~ remarkable success of these field nursery culture efforts (Griffin et al. 2012; Lirman et al. 2014; Lirman et al. 2010; Lohr et al. 2015) and the short term fate of individual outplants (Griffin et al. 2015; Mercado-Molina et al. 2015). These evaluations are based on tractable observations and measurements of tagged colonies over one to a few years also densities? Observations of condition, such as presence of disease? Please be more specific here. And what is the spatial scale here?? There is a much greater challenge in evaluating *Acropora* spp. abundance at the meso-scale (100's m² to hectares) due to ???? fragmentation, partial, and full colony **mortality**. ~~Partially as a result,~~ there is no information available to evaluate if evaluating this scale question (namely, can active population enhancement can 'move the needle' in affecting reef-scale population trajectories of Caribbean *Acropora* spp.?). We used a broad scale, low-**resolution** census technique (direct observation by snorkelers documented via handheld GPS; Devine et al. 2005; Walker et al. 2012) to evaluate both the long term (2005 – 2015) trajectory of Florida Keys *Acropora* populations undergoing ~~ongoing~~ acute and chronic disturbances as well as the question of reef-scale impact of population enhancement. These ~~acute~~ (some of these are chronic, not acute) disturbances included

Comment [A13]: Do you mean the level of treatment is insufficient??

Comment [A14]: Sentence not clear to me

Comment [A15]: What do you mean by broad scale? What do you mean by "low-resolution"-- mapping of individual colonies might be considered high resolution

multiple hurricanes in 2005, a severe cold thermal event in 2010, mild bleaching in 2011, a milder storm in 2012, and a severe warm thermal mass bleaching event in 2014 as well as ~~ongoing and substantial~~ effects of predation and disease (Williams & Miller 2012).

A conservation organization in the upper Florida Keys (Coral Restoration Foundation, CRF) has been propagating and outplanting *Acropora cervicornis* since 2003 (substantial numbers ~~thousands??~~ since 2011) and *A. palmata* since 2012 (substantial numbers ~~hundres?~~ ~~Thousands??~~ since 2014), although the number of outplants placed on the reef has varied ~~greatly~~ over time ~~according to the factors such~~ because of as funding levels, permitting restrictions, and damaging storms which required time for recovery of nursery infrastructure and cultured stocks, ~~and funding levels~~. This ~~long and~~ sustained effort combined with the availability of historic census information from a range of reef sites in the upper Florida Keys provides a novel opportunity to evaluate potential reef-scale effects of *Acropora* spp. population enhancement against a backdrop of ongoing chronic and acute disturbances in the reef environment. We compared trajectories of *Acropora* spp. density at reef areas which had and ~~versus~~ had not received ~~population enhancement efforts~~ outplants over appropriate time frames to evaluate the ~~reef-scale impact~~ effects of enhancement. We also compared ~~between~~ censuses of each site over longer term from ~~(2005/6 to 2014)~~ and the recent severe bleaching interval (2014 versus 2015) to provide a broad assessment of population trends and acute bleaching impacts ~~on Acropora spp. populations~~ in this region.

Comment [A16]: What distinction are you making between reef-scale and regional?

METHODS:

Sites targeted for this study were ~~originally chosen in (2005) prior to the onset of~~ before substantial population enhancement efforts began. Habitat maps (Lidz et al. 2006; Marszalek 1977) were used to identify shallow (< 5m) coral habitat areas in the upper Florida Keys. Targeted reef areas were restricted to less than 5m deep as observations at deeper depths on snorkel become less reliable. This depth range encompasses the core habitat for *A. palmata*, though *A. cervicornis* traditionally occupies a wider depth range. Most sites were surveyed once in 2005-7, once in 2013 or 14, and once in 2015 (Suppl. Table 1; Miller 2008; Williams 2013).

Comment [A17]: It would be interesting to have data on the efficacy of outplanting *A. cervicornis* over a depth gradient

Teams of two or three snorkelers addressed each ~~reef area~~ study site with the intent to observe the entire reef ~~surface area~~ via swimming sequential, parallel linear transects. The width of each transect was adjusted according to ~~site~~ conditions including depth, relief and water visibility, with the intent ~~that the benthos was thoroughly observed with minimal~~ to avoid overlap. In practice, this is very challenging to accomplish and several practices~~??~~ were implemented do you mean several different techniques were tried or adjustments made? as the effort progressed to improve the practical coverage, including the delineation of the target area (or subset assigned to an individual snorkeler) with weighted dive flags, the use of compasses and pre-agreed headings (generally following the direction of reef spurs) to maintain parallel tracks. In the early censuses, dive scooters (SeaDoo VS Supercharged) were used, but snorkelers performed surveys predominantly under their own power in 2013-15.

Each snorkeler towed a handheld GPS unit (Garmin GPS72 in 2005-7; Garmin eTrex20 for 20113-15) in a waterproof plastic pouch attached to a floating dive flag. The GPS recorded the 'track' traversed by the snorkeler. When an *Acropora* ~~spp.~~ colony was encountered, the snorkeler recorded a waypoint on the GPS for each, and recorded the species ~~for each waypoint~~

on a field data sheet. In some cases, *A. palmata* and *A. cervicornis* colonies were observed growing in high density patches wherein it was not feasible to demarcate individual colonies. In these cases, the snorkeler would swim around the perimeter of the feature and record waypoints along the outline which were designated on the data sheet as a thicket. The area occupied by designated thickets was examined over time.

Comment [A18]: Not quite sure what you mean here-- do you mean the actual area of each thicket within the outlines?

After a survey was completed, the GPS-recorded track was saved. Waypoints and tracks were downloaded to a personal computer after each day of censusing and exported to a spreadsheet file, where the waypoint attributes were entered from the field data sheet. For each study site, maps were created in ArcGIS plotting the colonies and thickets observed for each census year (Fig 1A-1C). Lastly, the observational paths followed by the surveyors (i.e. the GPS tracks) were imported to each map to depict the area searched. Using the *Minimum Bounding Geometry* tool, the minimum area covered by the observational path (Observed area) was determined for each year*site map.

For each site, maps were then merged to make temporal comparisons for reef scale density trends; a long-term interval from the periods 2005-07 to 2013-14 (Fig 1D), and a short term interval from 2014 to 2015, over a severe thermal stress event in summer 2014 (Fig 1E). Each temporal comparison was restricted to congruent observed areas of the reef (i.e., covered by the observational tracks in both time points) by clipping the area of comparison to the area of overlap in the observed area for each year using the Intersect tool. If the congruent area consisted of numerous overlapping polygons, then the *Merge Polygon* tool was used. The area outlined as *A. palmata* 'thicket' was calculated at each time point and the number of colonies in each thicket was estimated using a standard density estimate of 1 colony per m² (based on

Comment [A19]: So, it was not possible to determine if there were decreases or increases in density within thickets, correct--- Were outlines of the thickets compared over time to check for increases/decreases at the edges??

independent field estimates using fixed area belt transects at Horseshoe reef over four years yielding a mean of 1.01 ± 0.26 SD colonies per m^2 ; M.Miller unpublished data). Individual colony waypoints and thicket abundance estimates were summed for each species to obtain the total abundance for each survey year in the overlapping comparison area. This number of colonies of each species in each year in the congruent search area of reef was converted to density (total number of colonies observed / congruent observed area of reef (m^2)) to compare between time points (Mann-Whitney Rank Sum tests). For temporal comparisons, the proportional change in density between two time points was calculated.

Information on the total number of coral fragments of each species outplanted to each censused reef site by year was provided by staff of the Coral Restoration Foundation (J. Levy and K. Ripple; Pers comm). CRF is the only organization undertaking large scale *Acropora* spp. population enhancement in this region. The change in mean density over the longest observed interval for each reef (Suppl. Table 2) was used to evaluate the overall impact of population enhancement for *A.cervicornis* as outplanting has been ongoing for this species since 2008 and this enabled the use of information from all sites ($n=14$, a few of which had not been surveyed in 2013 or 14). However, substantial outplanting was only conducted for *A.palmata* since 2014 so the 2014 to 2015 interval only was used to evaluate outplanting effect for this species. For each species, we conducted a Mann-Whitney rank sum test comparing proportional change in colony density between the sites which had and sites which had not received outplants over the relevant interval. Also, a simple linear regression was performed for each species between the proportional change in colony density and the cumulative number of outplants among all sites.

Comment [A20]: It would be best to make this clear much earlier in the paper---the reader will be assuming all along that both species were considered for this early, longer time period

RESULTS:

The total surveyed area for each interval ranged from 55 to 77 hectares while the congruent observed area of reef for temporal comparisons within each site ranged from 1.6 to 15.5 hectares (Table 1). *Acropora palmata* thickets were observed at four sites in 2006-7, two of ~~these thickets which~~ had disappeared by 2015. At these two sites (Grecian Rocks and Watson's Reef) the aggregation of *A.palmata* colonies in the thicket area had dwindled to where it was no longer designated a thicket, though a few ~~remnant~~ colonies remained. One of the other two thickets showed approximately ~~half~~ 50% decline in area, whereas the last was approximately stable in area (Fig 2). Overall, this represents over two thirds loss in total *A.palmata* thicket area among these four sites.

~~In the interval from~~ Between 2006 to 2014, *A.cervicornis* showed a substantial ~~positive~~ change-increase in density when averaged across all surveyed sites (n=9) with the most dramatic changes occurring at sites receiving outplants (Table 1A, Fig 3A). In contrast, ~~average?~~ *A.cervicornis* density was essentially stable ~~on average~~ between 2014 and 2015 (co-incident with a mass thermal bleaching event and a smaller cumulative number of outplants) yielding a significant difference in density change between the two intervals (Mann-Whitney Rank Sum Test $p=0.024$; Table 1, Fig 3A). Meanwhile, *A.palmata* showed much smaller proportional changes in density (corresponding with much fewer total outplants; Table 1, Fig 3). While the average trend was substantially negative in the 2006-14 interval and essentially stable in the 2014-15 (bleaching) interval (Fig 3), this difference was not statistically significant.

Comment [A21]: I must have missed something but I am having difficulty figuring out just how the thicket areas were assessed/estimated/handled

Comment [A22]: Please provide some idea of the areal extent involved here

To specifically evaluate the hypothesis that outplanting effort had a significant, landscape-scale effect on colony density, we performed two separate tests; for *A.cervicornis* these tests were applied to the full interval of observation at each site (2005-2015, n=14 sites, Suppl Table 2) whereas for *A.palmata*, substantial enhancement effort has only occurred since 2014 so the 2014-2015 interval was used. A Mann-Whitney U-test indicated that sites receiving *A.cervicornis* outplants had significantly different change in density than those that did not ($p=0.004$). However, no significant difference occurred for *A.palmata* (corresponding to a much smaller cumulative number of outplants, Table 1). Simple linear regression showed a strong and highly significant relationship between change in *A.cervicornis* colony density and cumulative number of outplants among sites (Fig 4A). The similar regression for *A.palmata* for the 2014-2015 interval when outplanting (as well as the bleaching event) occurred showed no relationship (Fig 4B).

DISCUSSION:

Our low resolution but large scale survey approach was repeated over multiple reef sites over a decadal time frame in which both extensive population enhancement effort and an acute thermal disturbance (along with several lesser disturbances) occurred. Thus, this approach was designed to detect large changes at a large spatial scale. Our surface-based observation method restricted mapped areas to less than 5m depth. Although the historic core habitat of *A.cervicornis* likely extended deeper than this, current known distribution of *A.cervicornis* in the Keys is predominated by nearshore (shallower) habitats in contrast to the deeper fore-reef habitats historically described for this species (Miller et al. 2008). Thus,

although extensive *A.cervicornis* distribution in deeper areas not covered by our study is possible, current evidence does not support this in the Florida Keys.

Much greater overall enhancement effort went to *A.cervicornis* in comparison to *A.palamta*, and this added effort corresponded to a significant landscape scale effect. *A.cervicornis* showed a significant and positive relationship with the degree of this enhancement effort across sites over the entire study period (Fig 4A). However, the acute thermal bleaching event appears to have overcome even the enhancement effort and yielded no discernable change between 2014 and 2015 (Fig 3) in spite of ~ 1500 outplants occurring across the surveyed sites. Both the overall densities and the scale of the enhancement effort have been smaller for *A.palamta* (Table 1) which shows a clear pattern of declining density over the recent decade both overall (Fig 3B) and as represented in the occupation of thickets (Fig 2). This mostly negative population trend has not been substantively overcome by the small outplanting effort to date.

The resolution of our survey technique was low, as the challenge of a snorkeler navigating in open ocean as well as variation in depth, visibility, and likely individual observer variation yielded less than perfect observational coverage and detection of colonies ~~that were present~~. However, we implemented improved field techniques ~~over time~~ which improved the operational coverage of the area surveyed (e.g. the deployment of surface markers to delineate the survey area for each surveyor and the use of compasses) over time (e.g., compare coverage of tracks in Fig 1A vs 1B). Thus, results suggesting overall decline in densities are conservative as our observational detection should have been improved in later years. Also, this technique allowed us to evaluate population trends at a hectare scale. More resolved ~~????~~ techniques

Comment [A23]: Correct spelling throughout

Comment [A24]: But what about compared to 2007???

such as photo mosaics provide a much more precise assessment technique, but are still only applicable at meso-scales (hundreds of m²; Lirman et al. 2007)).

The substantial loss of *A. palmata* thicket area is a particularly concerning result.

Acropora thickets are understood to have been the typical configuration on Caribbean reefs prior to the drastic decline of these species starting in the late 1970s early 1980's (Goreau 1959; Gladfelter 1982, Jaap 1984) and are functionally important in terms of providing structural habitat both for other reef inhabitants and to facilitate fragment retention (i.e., successful asexual reproduction) for the coral itself. This importance is reflected in the fact that area of thickets (not just population abundance) has been defined as a key criterion for determining the recovery of these species under the US Endangered Species Act (NMFS 2015). The loss of *A. palmata* thicket area thus represents a trend opposing species recovery. The density of all *A. palmata* colonies also shows negative trends at most sites, both before and during the acute thermal bleaching event (Table 1). These alarming results emphasize the need for continued enhancement effort and development of approaches to more effectively convert *Acropora* spp. outplants into thickets.

Overall, population enhancement is associated with reef-scale positive trends in *Acropora cervicornis* in the Florida Keys. Unfortunately, this effect can be overpowered by massive thermal stress events such as was experienced in this region in 2014-15. These results point to the necessity of ongoing population enhancement efforts to foster species recovery (as mandated by the Endangered Species Act) but also to the insufficiency of current strategies in a rapidly warming ocean where future climatologies are unlikely to resemble those of the recent past (van Hooidonk et al. 2013). The identification of thermal resistance traits in corals and

Comment [A25]: Perhaps unnecessary to state this

Comment [A26]: Have any efforts been made to do this? It is hard to visualize these outplants and no information is provided on just how they were done

Comment [A27]: But what about *A. cervicornis* thickets? More discussion of these is needed. Do they function the same way as *A. palmata* thickets??

their mechanisms is crucial ~~in order~~ to devise additional ~~assistive~~ strategies to enhance the thermal resilience of threatened corals.

Comment [A28]: But of course there are other stressors like diseases, predation, hurricanes

ACKNOWLEDGEMENTS: Funding for this project was provided by NOAA's Coral Reef Conservation Program. Field assistance by KL Kramer, A Valdivia, AJ Bright, R Pausch, L Richter, and M Connelly is gratefully acknowledged. R Pausch provided assistance with figure preparation. The Coral Restoration Foundation graciously provided information on total population enhancement by reef.

REFERENCES

- Devine B, Rogers CS, and Loomis C. 2005. Mapping marine populations: using surface water GPS for spatial analysis. *Proceedings of the Gulf and Caribbean Fisheries Institute* 56:411-420.
- Epstein N, Bak RPM, and Rinkevich B. 2003. Applying forest restoration principles to coral reef rehabilitation. *Aquatic Conservation: marine and freshwater ecosystems* 13:387-395.
- Goreau TF. 1959. The ecology of Jamaican coral reefs: I. species composition and zonation. *Ecology* 40:67-90.
- Griffin JN, Schrack EC, Lewis K-A, Baums IB, Soomdat N, and Silliman BR. 2015. Density-dependent effects on initial growth of a branching coral under restoration. *Restoration Ecology* 23:197-200.
- Griffin S, Spathias H, Moore T, Baums I, and Griffin B. 2012. Scaling up Acropora nurseries in the Caribbean and improving techniques. *Proceedings of the 12th International Coral Reef Symposium*. p 1-5.
- Jaap WC. 1984. *The ecology of the south Florida coral reefs: a community profile*: US Fish and Wildlife Service, FWS/OBS-82/08.
- Johnson ME, Lustic C, Bartels E, Baums IB, Gilliam DS, Larson L, Lirman D, Miller MW, Nedimyer K, and Schopmeyer S. 2011. Caribbean *Acropora* Restoration Guide: Best Practices for Propagation and Population Enhancement Arlington, VA.: The Nature Conservancy. p 54.
- Lidz BH, Reich CD, Peterson RL, and Shinn EA. 2006. New Maps, New Information: Coral Reefs of the Florida Keys. *Journal of Coastal Research*:260-282.
- Lirman D, Gracias NR, Gintert BE, Gleason ACR, Reid RP, S. N, and P. K. 2007. Development and application of a video-mosaic survey technology to document the status of coral reef communities. *Environmental Monitoring and Assessment* 125:59-73.
- Lirman D, Schopmeyer S, Galvan V, Drury C, Baker AC, and Baums IB. 2014. Growth Dynamics of the Threatened Caribbean Staghorn Coral *Acropora cervicornis*: Influence of Host Genotype, Symbiont Identity, Colony Size, and Environmental Setting. *PLoS ONE* 9:e107253.
- Lirman D, Thyberg T, Herlan J, Hill C, Young-Lahiff C, Schopmeyer S, Huntington B, Santos R, and Drury C. 2010. Propagation of the threatened staghorn coral *Acropora cervicornis*: methods to minimize the impacts of fragment collection and maximize production. *Coral Reefs* 29:729-735.
- Lohr KE, Bejarano S, Lirman D, Schopmeyer S, and Manfrino C. 2015. Optimizing the productivity of a coral nursery focused on staghorn coral *Acropora cervicornis*. *Endangered Species Research* 27:243-250.
- Marszalek DS. 1977. Florida reef tract marine habitats and ecosystems: Maps published in cooperation with State of Florida Department of Natural Resources. . New Orleans Outer Continental Shelf Office: US Department of Interior Bureau of Land Management
- Mercado-Molina AE, Ruiz-Diaz CP, and Sabat AM. 2015. Demographics and dynamics of two restored populations of the threatened reef-building coral *Acropora cervicornis*. *Journal for Nature Conservation* 24:17-23.
- Miller MW. 2008. Acropora Spatial Survey Data of the Upper Florida Keys National Marine Sanctuary 2005 -2007. (NODC Accession 0046934). . NMFS InPort Catalog ID # 24327; <https://inport.nmfs.noaa.gov/inport/item/24327>.
- Miller MW, Lohr KE, Cameron CM, Williams DE, and Peters EC. 2014. Disease dynamics and potential mitigation among restored and wild staghorn coral, *Acropora cervicornis*. *PeerJ* 2:e541.
- Miller SL, Chiappone M, Rutten LM, and Swanson DW. 2008. Population status of *Acropora* corals in the Florida Keys. *Proceedings of the 11th International Coral Reef Symposium* 2: 781-785
- NMFS. 2015. Recovery Plan for Elkhorn (*Acropora palmata*) and Staghorn (*A.cervicornis*) Corals. Prepared by the Acropora Recovery Team for the National Marine Fisheries Service. Silver Spring, Maryland.

- Rinkevich B. 2015. Climate Change and Active Reef Restoration—Ways of Constructing the “Reefs of Tomorrow”. *Journal of Marine Science and Engineering* 3:111-127.
- Schopmeyer SA, and Lirman D. 2015. Occupation Dynamics and Impacts of Damselfish Territoriality on Recovering Populations of the Threatened Staghorn Coral, *Acropora cervicornis*. *PLoS ONE* 10:e0141302.
- van Hooidonk R, Maynard JA, and Planes S. 2013. Temporary refugia for coral reefs in a warming world. *Nature Clim Change* 3:508-511.
- Walker BK, Larson EA, Moulding AL, and Gilliam DS. 2012. Small-scale mapping of indeterminate arborescent acroporid coral (*Acropora cervicornis*) patches. *Coral Reefs* 31:885-894.
- Williams DE. 2013. CRCP-*Acropora* spp. distribution in the upper Florida Keys 2013-2015. NMFS InPort Catalog ID# 26791; <https://inport.nmfs.noaa.gov/inport/item/26791>.
- Williams DE, and Miller MW. 2012. Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys (USA). *Coral Reefs* 31:369-382.
- Young CN, Schopmeyer SA, and Lirman D. 2012. A review of reef restoration and coral propagation using the threatened genus *Acropora* in the Caribbean and Western Atlantic. *Bulletin of Marine Science* 88:1075-1098.

Figure Legends:

Fig 1: Component maps and spatial analyses are illustrated for a single site, Grecian Rocks; a similar sequence of maps was constructed for each site and temporal comparison. Observed search tracks and waypoint features mapped for each census year (2006 points as stars, 2014 points as asterisks, 2015 points as triangles) are given in A)-C) with *A. palmata* colony waypoints depicted in yellow, *A. cervicornis* colonies in purple, and *A. palmata* thicket outline points in orange. D-E) Merged maps for two temporal comparison showing the common observed area (determined by GIS intersect of the polygons determined by the search tracks for each year) for both years and the overlayed colony distribution observed in both years.

Fig 2: Area (m^2) of *A. palmata* thickets (i.e. high density aggregations for which mapping individual colonies was deemed infeasible) at four sites over time. Horseshoe was surveyed in both 2005 and 2007 so the point for this time period is a mean of these two. Thickets dropping to zero area likely still contained remnant colonies, but at lower densities such that individual colonies could be mapped (see text for details on methods).

Fig 3: Proportional change in colony density (mean plus 1 SE; n=9 sites) for *Acropora cervicornis* (A) and *Acropora palmata* (B) during two time intervals. Right y-axis shows the cumulative number of fragments of each species outplanted to these sites during the same intervals. Note the differences in axis scales.

Fig 4: Scatterplot showing linear regressions for change in colony density relative to the cumulative number of outplants for A) *Acropora cervicornis* (full interval of observation, n=14 sites) and B) *Acropora palmata*. Population enhancement has only occurred for *A. palmata*

since 2014, so B) shows proportional change in density for this species from 2014-2015 at $n=9$ sites (regression is not significant).