4-26-2019

Optimizing restoration site selection along the Florida Reef Tract for the coral species Acropora cervicornis and Acropora palmata

Samantha King
Nova Southeastern University, sk1318@nova.edu

Thesis of
Samantha King

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

April 2019

Approved:
Thesis Committee

Major Professor: Joana Figueiredo, Ph.D.

Committee Member: Brian Walker, Ph.D.

Committee Member: Emmanuel Hanert, Ph.D.

NOVA SOUTHEASTERN UNIVERSITY

HALMOS COLLEGE OF NATURAL SCIENCES AND OCEANOGRAPHY

Optimizing restoration site selection along the Florida Reef Tract for the coral species *Acropora cervicornis* and *Acropora palmata*

By:

SAMANTHA KING

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

Thesis of
Samantha King

Submitted in Partial Fulfillment of the Requirements for the Degree of

Master of Science:
Marine Biology

Samantha King

Nova Southeastern University

Halmos College of Natural Sciences and Oceanography

May 2018

Committee approval

_____

Dr. Joana Figueiredo, Major Professor

_____

Dr. Emmanuel Hanert, Committee Member

_____

Dr. Brian Walker, Committee Member

TABLE OF CONTENTS

List of Figures

List of Tables

List of Equations

Abstract

The decline of *Acropora cervicornis* and *Acropora palmata* populations and consequent listing as endangered species has prompted the need for restoration. Since financial resources are limited, optimal sites for restoration should not only be environmentally suitable for outplant survival, but also have a greater capacity to replenish surrounding reefs with larvae. However, in Florida coral larval dispersal patterns and reef connectivity remain poorly studied. Here, we measured long term larval survival and competency of *A. cervicornis* to calibrate a high resolution (100m) biophysical larval dispersal model of *Acropora* in the Florida Reef Tract (FRT). This model revealed that there is potential connectivity between reefs along the FRT, with most source reefs being located in the southern portion of the reef track, and most sinks in the northern part. The connectivity matrix was used then to develop a metapopulation model accounting for larval dispersal patterns, current and historic habitat for the species, growth, fecundity, and density-dependent post-settlement mortality for *A. cervicornis* and *A. palmata*, which allows comparing the capacity of suitable restoration sites to recolonize other reefs through sexual recruitment. Furthermore, it can determine optimal mesoscale spatial scaling and temporal planning of restoration project. We found that there was regional variation in the optimal spatial scaling, due to differences in intra-reginal connectivity and exiting coral cover. We also found that temporally staggering outplanting effort is important in poor environmental conditions. Considering ecological processes in restoration will enhance genetic diversity, hasten coral recovery, and boost resilience across the entire reef system.

Keywords: Metapopulation modelling, Connectivity, SLIM, Recruitment, Outplanting

Introduction

Tropical coral reefs provide numerous ecological services and are economically significant globally. Corals provide habitat for numerous species of fish and invertebrates; generating biodiversity hot spots and rendering coral reefs as indispensable sources of food and income for coastal communities worldwide (Cesar et al. 2003). Their economic value derivates from services such as, but not limited to, tourism, recreational and commercial fishing, and medicinal resources (Spurgeon 1992, Moberg and Fo1ke 1999). Due to these services, the Florida Reef Tract (FRT) has an estimated asset value of 8.5 billion USD (NOAA). Furthermore, reefs mitigate wave energy, protecting coastal areas from tides, waves and storm action. This limits beach erosion and flooding in the heavily developed coastlines bordering coral reefs (Moberg and Folke 1999, Ferrario et al. 2013). Coral reefs also shelter mangrove environments, which act as nurseries for countless commercially valuable pelagic and reef fish (Nagelkerken et al. 2000). Therefore, coral reefs are crucial not only for maintaining ocean health and biodiversity, but as an economic resource to communities around the world.

Despite their global significance, coral reefs are declining due to a combination of natural and anthropogenic stressors. Anthropogenic stressors can impede corals from coping with natural stressors, such as disease, predation, competition with macroalgae, and storm damage; whist increasing the prevalence of these natural events (Williams and Miller 2012, Randall and van Woesik 2015, Cheal et al. 2017). Additionally, global and local anthropogenic stressors, such as ocean warming and acidification, overfishing, sedimentation, pollution, and nutrient enrichment, curtail recovery of coral populations (Hunte and Wittenburg 1992, Hughes et al. 2003, Albright 2010, Spalding and Brown 2015). These stressors not only affect the health and growth of corals (Renegar and Reigl 2005, Hoegh-Guldberg et al. 2007), they impact all their life stages: reproductive output, fertilization, larval settlement metamorphosis, recruitment, and the survival of juveniles (Hunte and Wittenburg 1992, Munday et al. 2008, Albright 2010, Hoey et al. 2016, Fourney and Figueiredo 2017). Thus, limiting nearly every facet of a population's capacity to recover and remain genetically diverse, while simultaneously forcing populations to rely on asexual modes of reproduction (i.e. growth, fragmentation and reattachment), of which success is more reliant on the absence of stressors (Albright 2010). The shift in reproductive mode from

sexual to exclusively asexual decreases the capacity to maintain genetic diversity within the populations; reducing the populations' capacity to cope and adapt to environmental changes (Baums et al. 2006). As high mortality and low recruitment continues, the ensuing overall reduction in living tissue will diminish the size and number of sexually mature colonies, resulting in even lower sexual output by the populations, furthering their decline (Williams and Miller 2012).

However, if anthropogenic stressors are reduced, corals have the capacity to recover naturally if anthropogenic stressors are reduced. With good local environmental populations should recover on their own within ten years (Edwards 2010, Gilmour et al. 2013). As coral health improved, corals would grow faster asexually, aiding population recovery. In branching species, asexual reproduction can also arise through fragmentation and reattachment of the resulting propagules, which can be vital after a disturbance event (Lirman 2000). Therefore, if there is high survival and recruitment following a disturbance event, followed by high local retention, even poorly connected reefs can increase their biomass and cover to pre-disturbance levels (Gilmour et al. 2013).

While asexual reproduction can lead to rapid increases of the population size, recovery through sexual reproduction is essential for maintaining and increasing genetic diversity and connectivity across the entire reef system. By providing the raw material for adaptation and acclimation, genetic diversity can be vital for allowing populations to persist through environmental stressors and changes, (Baums et al. 2006, Drury and Lirman 2017). Reefs are connected through the exchange of larvae. The larvae (planulae), are planktonic and will remain in the water column until competency is acquired (the ability to settle and metamorphose) and a suitable reef for settlement is found (Richmond and Hunter 1990). Planulae select habitat by responding positive and negative settlement cues, such as the presence crustose coralline algae, bacterial biofilms, macroalgae, light, and reefs sounds (Mundy and Babcock 1998, Gleason et al. 2009, Kuffner et al 2006, Ritson-Williams 2009, Vermeij 2010). After settlement and metamorphosis, corals are referred to as recruits, these can be locally derived or from downstream sources (Burgess et al. 2014). The length of time larvae can survive and maintain competency are important determinants of the species range and distribution, as it directly influences how far from the paternal reef they can settle (Richmond and Hunter 1990). Lower

minimum times to competency result in higher rates of local retention (Figueiredo et al. 2013). However, for many species, the length of time larvae can survive and maintain competency is unknown because laboratory studies typically provide the larvae with continuous settlement cues (Connolly and Baird, 2010). These factors determine the species' range and distribution, as it directly influences how far from their natal reefs they can settle (Richmond and Hunter 1990). Additionally, with rising ocean temperatures, the time for larvae to reach competency is reduced, which would cause increased settlement on parental reefs (Figueiredo et al. 2014). Thus, sexual reproductive output and larval biology and ecology have a major influence in the broad scale connectivity of reefs and are relevant for both reef recovery and the maintenance of genetic diversity (Treml et al. 2012).

The decline of coral populations worldwide has prompted the need for active coral restoration (Rinkevich 2008). Typically, this is performed by growing coral fragments in *in situ* nurseries, and outplanting them on a reef (Epstein et al. 2001). These methods have been shown to significantly increase local coral cover (Young et al. 2012, Miller et al. 2016). Currently, outplanting is ineffective at a large scale, taking a notable amount of time and manpower, equating to high costs for minimal returns on the broad scale of the system's recovery (Young et al. 2012). Currently, site selection for restoration is based on ease of access, the availability of hard substrate, low predator and competitor abundance, water quality, light levels, or the presence of adult or juvenile colonies (Edwards 2010, Johnson et al. 2011). Oftentimes, genetic diversity nor site's intake and contribution of larvae are considered, despite both being recommended by restoration manuals (Edwards 2010). However, until larval output known, outplant sites will remain selected solely based upon environmental factors, with no considerations of genetic diversity and larval dispersal; thereby diminishing the possible widescale influence that active restoration could provide, especially in severely diminished populations like Acropora in the Atlantic.

Since the 1980s, *Acropora cervicornis* and *Acropora palmata* have experienced severe population declines (Goreau 1959, Aronson and Precht 2001), despite being the dominant reef builders of the Florida Reef Tract since the Pleistocene (Miller 2002). This decline occurs in spite of their rapid growth rate (Gladfelter et al. 1978), which has allowed them to create structurally complex habitats for numerous invertebrates and fish for thousands of years

(Pandolfi and Jackson 2006). Losses upwards of 97% in some areas (Miller et al. 2002), elicited their listing on the Endangered Species Act in 2006 as threatened and on the International Union for the Conservation of Nature as critically endangered (NOAA 2006, Aronson et al. 2008a, b). The deterioration of these species has led to structural instability on reefs and for countless coral reef inhabitants (Miller et al. 2002). Their protected status notwithstanding, and the major restoration efforts towards them, Florida's *Acropora* populations continue to decline. Their very low abundance, the monoclonal nature of the reef patches (having only one genotype, due to reliance on asexual reproduction, Williams et al. 2008), and the increased distance between patches, compounds the unlikelihood of gametes from different parental genotypes encountering, and fertilization ensuing (Lirman 2000). Even when fertilization is successful, larvae still need to find suitable settling habitat. The detection of appropriate substrate may, however, be impaired due to the current lack of reef structure (Lirman 2000, Gleason et al. 2009, Kuffner et al. 2009, Vermeij et al. 2010). The loss of coral cover often facilitates the preemption of free space by macroalgae, which can provide negative cues to coral larvae, further compromising the chances for successful recruitment (Kuffner et al. 2006). The well documented very low to non-existent larval recruitment in these *Acropora* spp. (Hughes and Tanner 2000, Lirman 2000, Williams et al. 2008), has forced them to solely rely on growth and fragmentation for natural recovery; causing the patches to be monoclonal. Understanding these species' connectivity patterns is vital for source reefs to be a key consideration in restoration and conservation; facilitating their genetic diversity, and thereby resilience to environmental stressors, to be increased (Thomas et al. 2015).

In the last 20 years, knowledge gaps in connectivity and larval dispersal of benthic organisms have slowly started being filled. This can be attributed to technological advances, as well as communal realization of the importance these ecological concepts have for population management. Moreover, as marine protected areas have become more commonplace, the need to monitor their effectiveness has necessitated understanding the demographic connectivity of the regions (Selig and Bruno 2010). Between 1998 and 2007, larval dispersal and connectivity studies increased to 10%, from the 0.7% they constituted in 1990, demonstrating the scientific need for them (Jones et al. 2009). During this time, different methodologies have been developed for varying spatial and temporal scales of interest. For instance, direct observations of larval behavior, genetic sampling, and the use of microchemistry are useful for small scale research

(Jones et al. 2009). However, as modelling capabilities have improved (Galindo et al. 2006, Wood et al. 2014, Gaggioti 2017), genetic and larval ecology data are increasingly combined with oceanographic information to determine dispersal (Hellberg 2007, Thomas et al. 2015), allowing for seascape wide views. Genetic connectivity models are useful for predicting the genetic structure of metapopulations, which allows for inferences on exchange. Whereas bio-physical dispersal models can be used to simulate the processes of dispersal and provide estimates on demographic connectivity and the factors controlling it (Cowen and Sponaugle 2009, Wood et al. 2014). Early studies often relied on additive diffusion modeling and passive particle models based on mean currents but were unable to account for realistic ocean conditions (Cowen et al. 2009). Now, high resolution hydrodynamic models are being generated that can account for small scale circulation, such as eddies around reefs, thus allowing for more realistic simulations of dispersal (Wood et al. 2014, Thomas et al. 2015, Mayorga-Adame et al. 2017). However, to be effective, high-resolution oceanographic models need to be combined with biological information regarding larval ecology and behavior, such as the survival, time to competency, loss of competency, and swimming abilities (Metaxas and Saunders 2009, Cowen et al. 2016, Mayorga-Adame et al. 2017, Legueux 2018). To date, long term competency and survival of some species of Scleractinian corals have been integrated into dispersal models (Connolly and Baird 2010), and even high resolution bio-physical dispersal models (Thomas et al. 2015), however no such studies have not been conducted with *Acropora* on the FRT. Studying larval ecology and hydrodynamics around reefs results in better understanding of the connectivity of the system and it's limitation to inform management in ways to protect and enhance natural reef recovery.

Current restoration efforts for *A. cervicornis* and *A. palmata* on the Florida Reef Tract primarily focus on increasing abundance and coral cover on localized outplant sites. In this study, long term survival and competency data were collected, and used to calibrate a high-resolution hydrodynamic model to determine connectivity estimates for Floridian *Acropora*. The resulting connectivity matrix facilitated the development of a metapopulation model, which was used to test different restoration scenarios to optimize restoration. Such scenarios that can be tested with the model include, but are not limited to, selection between environmentally favorable sites, temporal design, and spatial scaling of outplants so that restoration can simultaneously increase cover at both local and downstream sites through sexual reproduction

and connectivity. Additionally, this management tool would promote genetic diversity of the FRT promoting species' resilience in the face of the environmental changes.

Objectives

The purpose of this study was to assist management needs by developing a tool to optimize outplanting. Ultimately, the selection of restoration sites with considerations for connectivity would increase the genetic diversity and the resilience of Acroporids on the Florida Reef Tract. To fulfill this goal, three objectives were completed:

1. Determine the long-term survival and competency of Caribbean *Acropora* spp.
2. Identify source and sink reefs using a high resolution biophysical hydrodynamic model
3. Develop a metapopulation model to select optimal sites for restoration and spatial and temporal design of outplanting

Methodology

1. Study species and site

1.1. *Acropora cervicornis* and *Acropora palmata*

Staghorn coral *Acropora cervicornis* and Elkhorn coral *Acropora palmata* have dominated reef crests and shallow fore reefs (1-25m) in the Atlantic and Caribbean since the Pleistocene (Miller 2002, Baums et al. 2005, Aronson et al. 2008). *A. cervicornis* and *A. palmata* are hermaphroditic broadcast spawners, typically releasing their gametes a few days after the full moon of August (Richmond and Hunter 1990). After fertilization and a 72-hour developmental phase, the larval stage is reached. Planula are planktonic and lecithotrophic and usually become competent 4-5 days after spawning (Randall and Szmant 2009). As adults, these corals are characterized by many branching limbs, which are wide in the case of *A. palmata*, making them important for reef structure and habitat production. Their recent decline and importance to reef systems led to them being listed on the endangered species act. The recovery plan for these species includes using restoration to increase their abundance and preserve their genetic diversity

1.2. Florida Reef Tract

The Florida Reef Tract (FRT) is the third largest barrier reef system in the world. It extends 150 km from Stuart, Florida down to the Dry Tortugas on the edge of the Florida Straits (FDEP 2018). The outward limit of growth in some areas makes the reef nearly seven kilometers wide. The reef system is largely comprised of patch reefs and bank reefs (Marszalck et al. 1977). Reef development is most prolific seaward of the Florida Keys, where it is divided into three sections (Upper, Lower, and Middle Keys) based on geological formations and
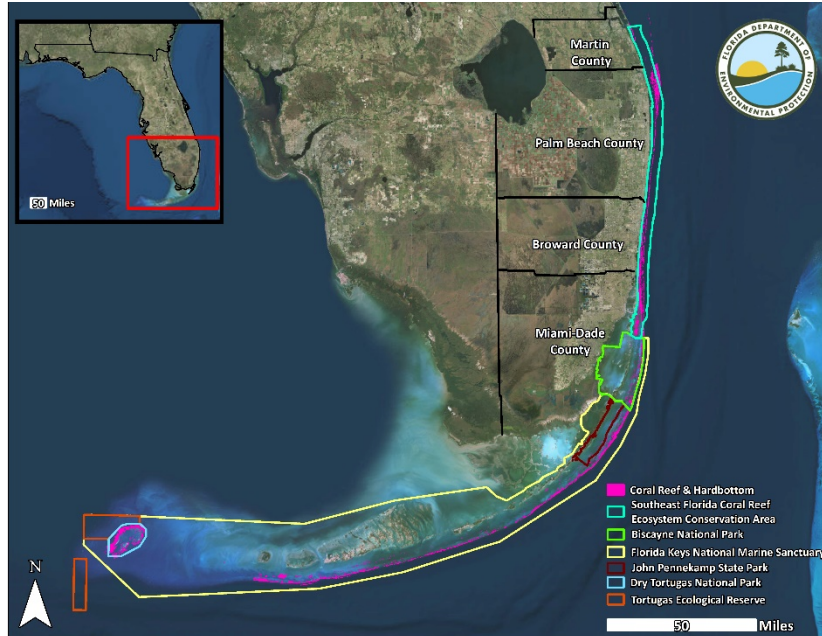
Figure 1: Map of the Florida Reef Tract (in pink) and the management regions.

historical reef growth (Ginsburg et al. 2001). The Upper and Lower Keys are mostly patch reefs with islands formed from Pleistocene reef limestone. The middle keys have less patch reefs and the islands are derived mainly from Holocene sediment. The FRT supports extensive recreational and commercial activities which provide multi-billion dollars of income to the region and supports thousands of jobs (NOAA 2016).

2. Larval Experimentation- Biological Parameters

2.1. Coral spawning

From August 9th through 12th of 2017, 30 gravid colonies of *A. cervicornis* were removed from their nursery trees and transported by scuba divers and rehung on a smaller tree so that each colony was solitarily hanging near the sandy bottom in an area referred to as "spawn alley" of the Coral Restoration Foundation Nursery in Tavernier, Florida. Each evening, divers placed mesh tents over each colony with a 50 mL falcon tube labeled with the genotype of the coral. Spawning was observed each night from multiple genotypes. After allowing each colony to release its bundles for 45 minutes, all falcon tubes were removed and brought to the boat by

some of the divers, while others remained behind to remove the mesh tents. The Falcon tubes were emptied into a five-gallon container in equal quantities, to prevent the overrepresentation of any one genotype. Fertilization was maximized by combining all genotypes collected. Fresh sterile seawater (FSW) was then added to the container to lower the sperm concentration to approximately 10^5 and 10^6/mL, preventing polyspermy. Once almost all the eggs had broken apart, the gametes were transported to the land-based lab in Tavernier (~30-minute boat ride). One hour following bundle break down, all eggs were repeated rinsed with FSW in a fat separator to remove sperm

2.2. Long term survival

Embryos resulting from the gametes spawned on the night of August 11th, (16 different genotypes) were used to assess long term survival and competency. Eight hours post fertilization, 50 embryos were randomly assigned to 16 100mL jars with filtered seawater and no settlement cues. The jars were placed in water baths kept at 29°C, the average summer seawater temperature in South Florida. Each day, a 100% water change was performed on the jar and the number of surviving larvae were counted. This process was performed for 26 days, when all the remaining larvae died due to inability to access the lab during the passage of Hurricane Irma in September.

2.3. Long term competency

To measure the competency dynamics, larvae were reared in five 2L plastic bowls at a concentration of <1 larvae/mL seawater in the absence of settlement cues. The bowls were kept in water baths at 29°C. Larvae were rinsed daily with FSW and a 100% water change was performed. Beginning four days post fertilization through 10 days post fertilization, then once a week for two weeks (days 17 and 24) four replicates of 20 larvae were randomly removed from the cultures and placed in a 100mL glass jar with a pre-conditioned tile. The pre-conditioned tiles were deployed at the NSU Layer Cakes Nursery for approximately 2 months prior to the start of the experiment, facilitating the development of natural settlement cues for corals from crustose coralline algae and their associated bacterial biofilms. After 24 hours, the number of larvae settled and metamorphosed was recorded to estimate the proportion of competent larvae each day.

2.4. Data Analysis

2.4.1 Survival Modeling

Survival data was modelled using the methods described by of Connolly and Baird (2010) and extended by Figueiredo et al. 2013 and 2014. In the generalized Weibull model, where mortality rate is given by:

$$\mu(t) = \frac{\lambda v (\lambda t)^{v-1}}{1 - \sigma (\lambda t)^v}$$

1. 1

Three parameters determine the shape of the model's curve: λ, is the scale parameter, v is the shape parameter, and σ is the location parameter. This produces a "bathtub shaped" curve, where mortality is high during the inital stages of development, decreases as the larvae age, and then increases again when their energy reserves are depleted.

The second model tested was the Weibull model, which is a special case of the generalized form. In the Weibull model, $\sigma \rightarrow 0$, so that there are only two parameters, producing a monotonic increase or decrease in mortality such that:

$$\mu(t) = \lambda v (\lambda t)^{v-1}$$

1. 2

Finally, when $v=1$, the Weibull model becomes equivalent to an exponential model with a constant morality rate over time such that:

$$\mu(t) = \lambda$$

1. 3

The parameters for each of these models were estimated using maximum log likelihood. Since the experimental design is interval censored, with no larvae removed from the study and sampled at fixed time points, the log likelihood is:

$$\sum_{t=t_i}^{t_f} \left([A(t-1) - A(t)] \log[P_a(t-1) - P_a(t)] \right) + A(t_f) \log[P_a(t_f)]$$

2.1

Where t is time in days, t_f is the last day larvae were censored, $A(t)$ is the total number of individuals still alive at time t, and $P_a(t)$ is the probablity of a individual being alive at time t such that:

$$P_a(t) = e^{-\int_{\tau=0}^{t} \mu_T(\tau)d\tau}$$

<div align="right">3. 1</div>

Within RStudio, the function nlminb was used to estimate the paramaters that maximized the log liklihood (MLL) for each model. To compare the models and determine which would be most adequate, the Akaike information crierion (AIC) were calculated:

<div align="center">AIC=2k -2(-MLL)</div>

<div align="right">4.1</div>

Where k is the number of parameters in the model and MLL is the negative maximum log liklihood for each model. The model with the best fit had the lowest AIC.

2.4.2 Competency Modelling

Following similar methodology to the survival modelling, competency data was modelled such that the probability of larvae being competent at a given day (t) is given by the probability that they already acquired competency and maintain it until time t:

$$\int_{\tau=t_c}^{t_j} ae^{-(\tau-t_c)}\, e^{-\int_{\gamma=\tau}^{t_j} \beta(\gamma)d\gamma}\, d\tau$$

<div align="right">5. 1</div>

Where t_j is a given day, t_c is the minimum competency time, the rate of competency acquisition is a, β is the rate of competency loss, and b is the scale parameter because larvae can only become competent after t_c, $a=0$ when $t < t_c$. After t_c, larvae become competent at a constant rate. Larvae assume competency at a constant rate, but loss can be modelled by either the Weibull or exponential models. Therefore, two models were tested:

$$\beta(t) = b\eta(bt)^{\eta-1}$$

<div align="right">6. 1</div>

and, the exponential, where there is a constant loss of competency, such that $\eta=1$ and:

$$\beta(t) = b$$

<div align="right">6. 1</div>

The generalized Weibull was not fit to the data, because the occurrence of two shifts in the rate of competency loss is biologically implausible.

The per capita rate of loss of competency can be modelled with a Weibull model or an exponential model. In the Weibull, competency can be lost any time after it has been acquired, the rate of loss of competency increases over time. The probability of being competent is given by:

$$\sum_{t=t_c}^{t_f} log \binom{n_t}{c_t} p_t^{c_t}(1 - p_t)^{n_t - c_t} \qquad 7.1$$

where

$$\binom{n_t}{c_t} = \frac{n_t!}{c_t!(n_t - c_t)!}$$

Where t_f is the final sampling day, n_t is the number of larvae sampled on a given day, c_t is the number of competent (settled) larvae, and p_t is the probability of competency. Similar to the survival modelling, the nlminb function in R was used to optimize the model parameters and minimize the negative log likelihood. The resulting MLL was used to calculate the AICs.

While calculated separately the final two models for mortality and competency can be multiplied to find the probability of being an alive and competent larva that then can be used in the biophysical dispersal model, such that if $t \geq t_c$,

$$\int_{\tau=t_c}^{t_j} e^{-\lambda t^\nu} * ae^{-(\tau - t_c)} e^{-\int_{\gamma=\tau}^{t_j} \beta(\gamma)d\gamma} d\tau \qquad 8.1$$

3. Connectivity

3.1. Biophysical dispersal model

The model used in this study was the Second-generation Louvain-la-Neuve Ice-ocean Model (SLIM, http://www.slim-ocean.be). This study expanded on the work done by Frys et al. 2017. The model uses a finite element method which allows for an unstructured mesh; thus, the resolution can vary spatially. In coastal areas where small scaled features dominate, a high

resolution of 100m can be used, but a coarse mesh (900m resolution) can be utilized in offshore areas with more uniform flow and large-scale processes. The high resolution is capable of capturing small scale circulation and retention processes, such as eddies that form around a reef, thereby greatly increasing the accuracy of the dispersal models. Models with coarse resolution around reefs can vastly overestimate connectivity and underestimate local retention (Cowen et al. 2000). Benthos classification for the model was taken from the Unified Florida Reef Tract Map (UFRT). GIS polygons labelled as either "hardbottom" or "coral" were considered reef sites. This resulted in 987 reef sites that were used to determine connectivity in the dispersal model.

In SLIM, hydrodynamic forcings were estimated from wind, tide, and large-scale circulation National Centers for Environmental predictions, OSU TOPEX/ Poseidon Global Inverse Solution, and HYCOM respectively. Since we used the 2D barotropic version of SLIM, the model was relaxed towards the depth averaged velocity obtained from HYCOM, as it is a 3D baroclinic model. The model was run to simulate 2 months of physical oceanographic data, with outputs recorded every simulated hour for the year 2010. Outputs were validated from observational data and several regional locations, as well as HYCOM values.

To simulate larval dispersal patterns, a Lagrangian particle tracker, an offline module of SLIM, was utilized. It employed a random walk formulation of the advection diffusion equation. The velocity outputs from SLIM provided the inputs for the particle tracker. The simulation began by seeding reef polygons with 1600 larvae per km^2 on August 24th, 2010. Live, competent "larvae", as determined in section 2, assumed to settle on the first reef they passed over and were then removed from the simulation. The resulting connectivity matrix records, for each reef, the number of larvae it had sent to any reef was recorded. This was then normalized as a proportion by dividing the number of outgoing larvae by the total number of larvae released (i.e. seeded) from the incoming reef. The SLIM model for the FRT and the particle tracking (Section 3.1) were developed and ran by Dr. Hanert's lab at UC Louvain, Belgium.

3.2 Matrix Variations

3.2.1 Historic *Acropora* Sites

The connectivity matrix output from SLIM, utilized all 987 sites from the UFRT map However, not all hardbottom substrates house coral, and not all coral habitat is suitable for

Acropora, this original simulation allowed for the larval dispersal, potential connectivity, and growth of the entire FRT to be represented. However, the backcountry area, can experience large variations in salinity and nutrients due to inputs from the Florida bay, and while it is useful to understand these regions influences, it is unlikely to ever be heavily populated with coral. Thus, a reduced version of the All Hardbottom Sites Connectivity Matrix was produced based on the historic habitat of *Acropora* (e.g. the Historic *Acropora* Sites Connectivity Matrix), to better represent the reef sites that are more suitable for settlement and recruit survival of Acroporids. The 95% *Acropora* habitat map from Wirt et al. 2015 was used to determine which sites would be kept.

To do this, latitude and longitude coordinates for the reef sites from the UFRT polygons used to generate the All Hardbottom Sites Connectivity Matrix were imported into GIS, along with the *Acropora* habitat .shp file. The clip function was used to eliminate any of the original reef coordinate points that were not within the historic habitat polygons. All reefs that were excluded from the habitat were then removed from the matrix entirely, so they could neither send nor receive larvae, such that new matrix contained 429 of the original 987 reefs. *Since A. cervicornis* and *A. palmata* have very similar life history characteristics, it was assumed that the larval survival and competency data for these two species would be very similar, thus the same connectivity matrix was used for both species.

3.3. Data Analysis

The following indexes were calculated for the *Acropora* connectivity matrix that was generated.

The source index (K_i), was determined by how connected a reef was such that:

$$K_i = N_i^{out} * \sum_{j=1}^{n} C_{ij} \hspace{3cm} 9.1$$

Where N_i^{out} is the number of reefs to which reef *i* sends larvae, and $\sum_i^j C_{ij}$ is amount of larvae it sends to those reefs. Therefore a reef that has the same number of connections, but sends less larvae, would have a lower K value than a reef which exports high quantities of larvae. Reefs with a higher source index provide greater value to the entire reef system.

The sink index (S_i), were determined similarly based on the input connections:

$$S_i = N_i^{in} * \sum_{j=1}^{n} C_{ji} \qquad\qquad 9.\,2$$

Where N_i^{in} is the number of reefs that reef i recieves larvae from, and $\sum_{j=1}^{n} C_{ji}$ is the quantity of larvae it receives.

Local retention is the proportion of larvae released from a reef that settle back on that reef given by:

$$P_{ret} = \frac{c_{i,i}}{\sum_{j=1}^{n} c_{i,j}} \qquad\qquad 9.3$$

Where c_{ii} are the proportion of larvae from reef i that settled on reef i, over the quantity of larvae that released on reef i.

Self-recruitment is the proportion of larvae that settle back onto its reef of origin out of all the larvae that settled there, i.e.:

$$P_{self} = \frac{c_{i,i}}{\sum_{j=1}^{n} c_{j,i}}$$

$$9.4$$

Where C_{ii} are the proportion of larvae from reef i that settled on reef i, over the quantity of larvae that settled on reef i.

Finally, the connectivity model can be used to quantify larvae lost from the system. This would be the proportion of larvae released from a reef which settle on other reefs and the local retention, or proportion of larvae released from reef i which settle on reef i, subtracted from 1.

$$P_{lost} = 1 - \sum_{j \neq i} \frac{c_{i,j}}{\sum_i c_{i,j}} - \frac{c_{i,i}}{\sum_i c_{i,j}} \qquad\qquad 9.5$$

4. Metapopulation Model

4.1. Metapopulation Model

A metapopulation model was created where coral cover of a reef over discrete time (t, years) was described as:

$$C_{i,t} = c_{i,t-1}\left[1 + R\left(\frac{A_i - c_{i,t-1}}{A_i}\right)\right] + sa\left[\sum_{k=1}^{n}\left(f\,\frac{c_{k,t-1}\left[1+R\left(\frac{A_k - c_{k,t-1}}{A_k}\right)\right]}{a}\right)l_{i,k}\right]\left[1 - \frac{c_{i,t-1}\left[1+R\left(\frac{A_i - c_{i,t-1}}{A_i}\right)\right]}{A_i}\right]$$

<div align="right">10.1</div>

Where $c_{i,t}$ is coral cover (area) on patch i at time t and $c_{i,t-1}$ is coral cover on patch i the year prior. R is the growth rate of a patch (mortality + growth), A is the area of a patch, s is the probability of a recruit to survive and mature, a is the mean area of a polyp, j is the number of reefs in the study, f is the average fecundity of a polyp (eggs produced), and $l_{i,k}$ is the connectivity between patch k and i (larvae transported from patch k to patch i). The values used for the parameters are described in 4.2 and are listed in Table 1.

For any given year, the coral cover is dependent on the coral cover from the previous year, the growth of the patch (accounting for growth and mortality), and recruitment success of the year prior. The first term of the equation calculates the growth and mortality of a reef that occurred during year t. Growth, is density dependent, i.e. at lower densities there will be a higher growth (lower mortality and quicker budding). This is due to low intraspecific competition for space, whereas at higher densities there is a lower growth (higher mortality, slower budding) due to increased competition for space. The second term represents new recruitment to the reef. The number of successful recruits is dependent upon the number of polyps on a reef that survived from the year prior (as seen by one minus the first term), polyp fecundity, and the ability of larvae to reach and survive on reef i. The ability of larvae to reach a reef is determined by the connectivity matrix from the biophysical dispersal model, which stipulates that larvae are both alive and competent when they arrive to a reef. Finally, for these settlers to be recruited into the population and preempt space, their post-settlement survival must be considered, as well as the space available on the reef, based on the free space from the current cover and the size of the polyp recruit. Of all these potential recruits, the following factors determine if recruits will increase a reef's coral cover in addition to its annual growth: live, competent larvae pass over the reef, the availability of free space on the reef, and recruit survival during the first year.

4.2 Model Parameters

Model parameters were gathered from previously published studies. Larval survival and competency data were not able to be collected for *A. palmata*, so the model parameters and

connectivity were used to represent both species of Acroporids, since they are known to have very similar life history traits. The initial percent coral cover was 0.018 and .008 calculated from the mean percent live cover density of *A. cervicornis* and *A. palmata* respectively at sites monitored by Steven Miller across the Florida Keys from 1999-2017. This value is on trend with losses experienced in the region, being about half the mean percent cover seen in Vargas-Angel et al. 2003 at 5%. Area of a reef (*A)* was the size of the polygon from the UFRT in m^2. Since *Acropora* are a simultaneous hermaphrodite, sperm should not be limited, therefore a sites fecundity can be assumed to be the average number of eggs produced by each polyp. 21 eggs per polyp was the value used in this model, as it was the mean value from previous fecundity studies looking at the number of eggs in the mesenteries, instead of egg volume (Szmant 1986, Soong 1991). Fecundity (*f)* was a constant, as there was no reasonable way to estimate the likely variances that could occur based on location and age class. The post settlement survival success of a recruit (*s)* was 3% based on long term survival of field recruits (Chamberland et al. 2015).

Surface area of a polyp (*a*) was greater than the actual area a polyp occupies on a branch of *Acropora*. Unlike other species of coral, there is considerable skeletal space between polyps, so it is important to consider this 'blank space' as part of the functional unit polyp in the metapopulation model, so as not to overestimate the number of polyps on a reef. Thus, to determine this area, on fragments of adult *A. cervicornis* corals from both Broward County and the Florida Keys National Marine Sanctuary, sections of fragments of different sizes and ages were measured for circumference and length over areas of homogenous diameter. The area was calculated and divided by the number of polyps in that area. Therefore, polyp area included the oral disk, corallites, and the space between corallites. The mean value of these measurements, $8.158 \times 10^{-8} \text{m}^2$, was used for *a*. Three different growth rates were determined with a wide range of values, so instead of selecting one rate, all three were used as proxies for environmental conditions, in that the method that led to the highest calculated growth rate was used as a proxy for very good environmental conditions, the middle value as good, and the lowest value as poor. Gladfelter et al. 1978 measured the linear extension of a colony as 0.07 myr^{-1}, this value would not encapsulate the growth of the patch required for the parameter. The highest value was 0.8135m^{2}y^{-1}, based on the mean change in area of the two *Acropora cervicornis* patches surveyed biannually in Broward County over 3 years (Walker et al. 2012), and the middle value was 0.3534 m^{2}y^{-1} , based on the mean change of perimeter of those same two patches. (Walker et

al 2012). Finally, the lowest value was 0.014 m^2y^{-1} based on the mean of the limited instances of increases in percent live cover in long term monitoring studies (Goergen et al. 2019). Hitherto these growth rates will be referred to as very good, good, and poor based on the environmental conditions for which they are acting as proxies. These values are summarized in Tables 1 and 2. All modelling was done in RStudio Version 1.0.136.

Table 1: Summary of the estimated values for each parameter in the metapopulation model

Parameter	Value
$C_{i,t=0}$	0.018 m^2 ; 0.008 m^2
f	21 eggs/polyp
a	8.158*10^{-8} m^2
s	0.03

Table 2: Estimated growth rates and their representative environmental condition

Growth Rate (R)	Environmental Conditions
0.014 m^2y^{-1}	Poor
0.3534 m^2y^{-1}	Good
0.8135 m^2y^{-1}	Very good

5. *Restoration Simulations*

5.1. Current Reefs Spawning

To determine the optimal location, temporal and spatial design of restoration sites, the model was first run without considering restoration efforts to establish a baseline of comparison for recovery. This simulation was performed with both species and acted as the baseline for comparison for all other restoration simulations. This, and all other outplant scenarios, utilized the Historic *Acropora* connectivity matrix, and an additional matrix which included only the reefs currently with coral cover able to export larvae. The outplant scenarios were then assessed based on their capacity to improve the outlook for the FRT relative to the baseline model.

To create the Current Reefs Spawning connectivity matrix, *Acropora* presence data collected in the past 20 years for monitoring purposes by NOAA, Dr. Steven Miller (NSU), and the Dr. David Gilliam's CRAMM lab (NSU) was utilized. For each species, GPS coordinates of reefs with presence records between 2012 and 2018 were imported into ARCGIS Pro. Since the data was pooled from a variety of surveys, multiple years were utilized to account for differences in monitoring frequencies. The Near Table function was used to "assign" presence at a site from the monitoring data to historic *Acropora* sites. Historic sites that did not match current presence sites had all their export values replaced with a 0. However, because all the reefs in the Current Reefs Spawning matrix could be seeded, the model assumed that 4 years after receiving larvae, a previously barren reef could start producing larvae. *Acropora* recruits have been found to become sexually mature within four years (Chamberland et al. 2016). Thus, in the simulation, four years after a barren reef was seeded, it could begin "spawning" by calling on the Historic *Acropora* matrix for that reef, instead of the Current Reefs Spawning Connectivity Matrix which had rendered it unable to export. For all the reefs, only the area that was "occupied" 3 years prior (i.e. the polyps that are 4 years old) could produce larvae.

5.2 Outplanting Optimization

The following simulations are examples of questions that could be answered using the metapopulation model for either species.

5.2.1 Site to Site comparison

The metapopulation model can be used to determine where outplanting would be most effective. For instance, if there were a few environmentally favorable sites but only funding to restore one of them, the model could be used to determine which site would provide the best contribution to improving the entire FRT. Simulations were run for scenarios where one of three reefs were restored. For each reef, simulations were run at the three growth rates to assess recovery in different environmental conditions. For *A. cervicornis* randomly selected reefs 87, 396, and 182 from the Historic *Acropora* matrix, located around Key Largo, hereafter referred to as A, B, and C, respectively. For *A. palmata*, we randomly selected reefs 253 (D), 296 (E), and 11 (F) were used from the historic matrix, located around the same area. To simulate restoration of a reef, the Current Reefs Spawning Matrix was edited to include the outplant site, meaning it included the site's original larval output from the Historic *Acropora* Matrix instead of the 0s of

the barren reef, initial cover was set to 100m^2. The simulations were also all run with 50m^2 of outplanting cover to assess the sensitivity of the model to the area restored. To represent outplant mortality, the initial outplant cover was reduced by 23% in year two of the simulation (based on Goergen et al. 2018). Additionally, to account for outplant stress or month of outplanting, during the first year the outplanted cover could not spawn but surviving coral the second year could.

5.2.2 Spatial Scaling of Restoration

The model was also used to determine optimal spatial scaling of restoration, specifically if it is more effective to outplant a smaller area (20m^2) at more reefs (n=15) or outplant larger areas (100m^2) at fewer reefs (n=3. To determine if optimal spatial scaling varies between regions, this simulation was run using reefs located in a region of the FRT with a higher cumulative source index (the Lower Keys, as determined by the connections index, section 3), and then compared with a simulation ran in reefs located in a region with lower cumulative source index (the Upper Keys). Within each region, two different scenarios were tested, with simulations run at the three different growth rates to assess recovery in different environmental conditions. All these simulations were run a second time at each growth rate with the initial covers changed to 10 m^2 and 15 m^2 to assess the sensitivity of the model to the initial cover. While it is known that the size of the outplant and the density they are outplanted on affects survival, it was assumed that in both scenarios the corals were planted in the same way, with only differences in the square footage outplanted. Therefore, the outplant survival and spawning stipulations were the same as those seen in 5.2.1 for both scenarios.

5.2.3 Successive Outplanting

To test this, we used five strong source sites, each from a different region of the reef tract. The connectivity matrix was edited as described in 5.2.1. so that in year one outplanted sites had 100m^2 of coral cover, and then in years two and three each reef received an additional 50m^2. In year one, each year outplanted corals experienced 23% mortality (as seen in 5.2.1 and 5.2.2). Survivors from the previous year were able to spawn, along with 4-year-old polyps when applicable. For comparison, in the second scenario there was only one outplanting event, in which the same 5 reef sites received 200 m^2 of outplanting in year one and experienced 23% mortality. The 200 m^2 equated to the same effort applied over three years in the successive outplanting scenario. The simulations were run at all three growth rates to assess recovery in

various environmental conditions and at lower outplanting areas of 50 m^2 in year one, 25 m^2 in years 2 and three for the successive outplanting scenario, and 100 m^2 for the one-time scenario to assess model sensitivity to the initial parameters.

5.3 Data Analysis

To determine the optimal location, temporal and spatial design of restoration, the results of each simulation were assessed based on the recovery improvement in recovery relative to the baseline simulation (no restoration). The number of years it took the mean percent cover of all the historic *Acropora* reefs to be greater than 50% was assessed and reported as the relative improvement in recovery time the scenario provided from the Current Spawning model. Fifty percent was used because it was the percent coral cover reefs on the FRT had in the 1970s, before the severe population decline (Garner et al 2003, Schutte et al. 2010). The mean percent cover of the FRT over 20 years and is reported as the increase relative to the baseline model

Results

1. *Survival and competency*

Survival was best fit with a Weibull model (Table 6), meaning the mortality rate was initially higher, but decreased over time (Figure 2).

Table 3: Survival model, number of parameters, optimized parameter values, the Maximum Log Likelihood (MLL), and Akaike Information Criteria (AIC) values.

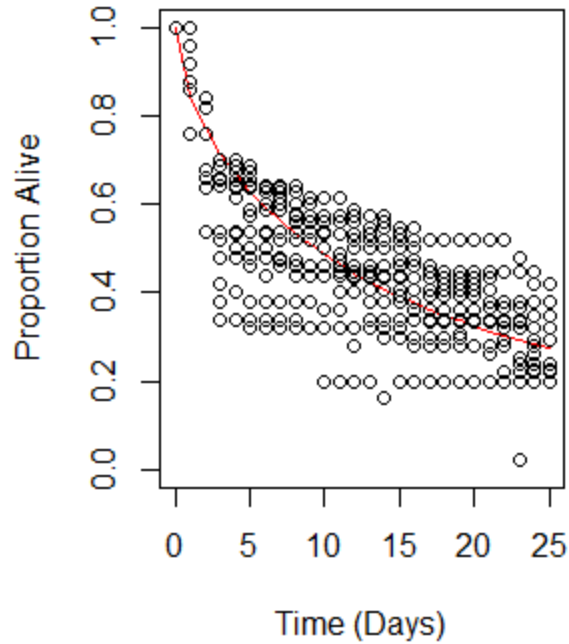| Survival Model	Parameters	λ value	ν value	MLL	AIC
Exponential	1	0.04301246	1	2044.144	4090.288
Weibull	2	0.06004278	0.6408791	2561.489	5126.978

Figure 1: Weibull survival curve for larvae survival over 26 days.

The fit of the exponential and Weibull loss of competency models were equivalent. The Weibull model was used, as it has previously been determined to model loss of competency in Pacific Acropora, when there was a longer period of data collection (*in prep,* Thomas and Figueiredo et al.). This means that the per capita rate of loss of competency was not constant over time (η=60.36698) (Table 6). Larvae began acquiring competency at 5 days (t_c=5.12), acquired competency at a constant rate (a=0.063).

Table 4: Competency models, the number of parameters included in the model, optimized parameter values, MLL, and AIC values.

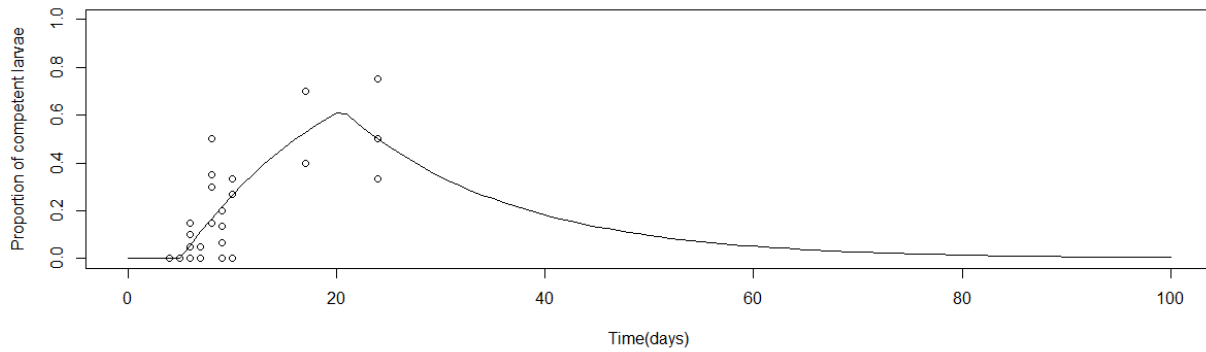| Loss of competency	Parameter	α	t_c	b	η	MLL	AIC
Exponential	3	124.7938	5.12699	0.016055	1	59.397	124.79
Weibull	4	0.063159	5.116213	0.0642704	60.367	58.731	125.46

Figure 2: Proportion of competent larvae over time.

As a result, the proportion of larvae that are alive and competent is null the first 5 days (tc=5.12), and then it increases, peaking around day 20, and then rapidly decreasing over time until around day 40, where it then slowly decreases (Figure 4).
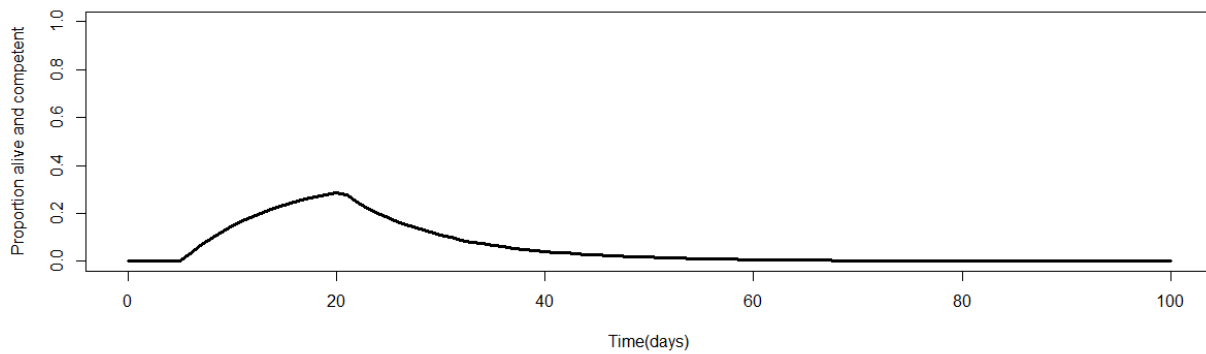

Figure 3: The proportion of larvae that are both alive and competent after spawning.

2. Connectivity Indexes

The larval dispersal showed that there was strong east and northward flow in the direction of the Gulfstream along all of the FRT, particularly in the more offshore reefs. High levels of intra-regional exchange of larvae occurred in that Lower Keys (Figure 6). The areas on the FRT which contained more source and sink sites, matched these findings, with the southern end having a greater quantity of sources, and the northern end containing more sink sites (Figures 6,7 8, 9, 10, and 11). The Lower Keys had the highest level of exchange, containing both sources and sinks, with some sites acting as both (Figure 11). The Dry Tortugas was not identified as either a source or a sink, as the dispersal model simulated most of its larvae being lost into the Gulf Mexico, instead experiencing local retention (Figure 6, 8, 14)
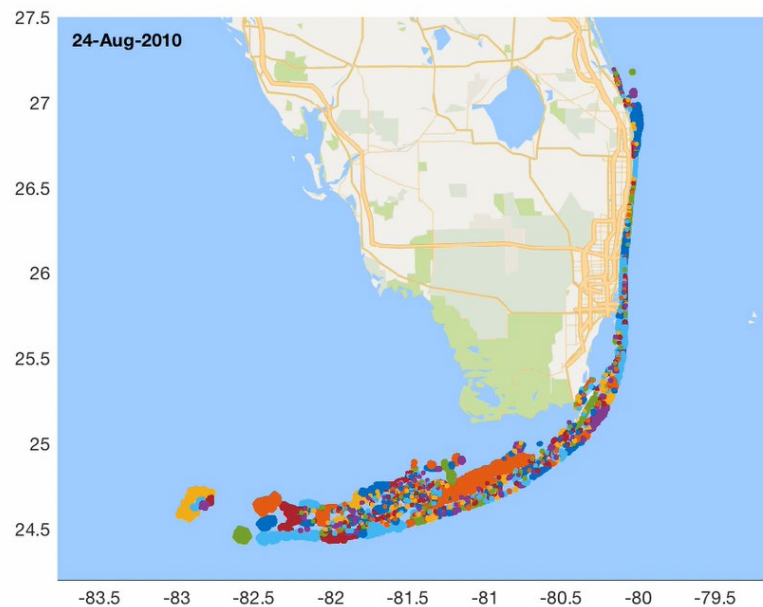
Figure 4: First day of the dispersal simulation. Colors depict dispersal kernels from each reef.
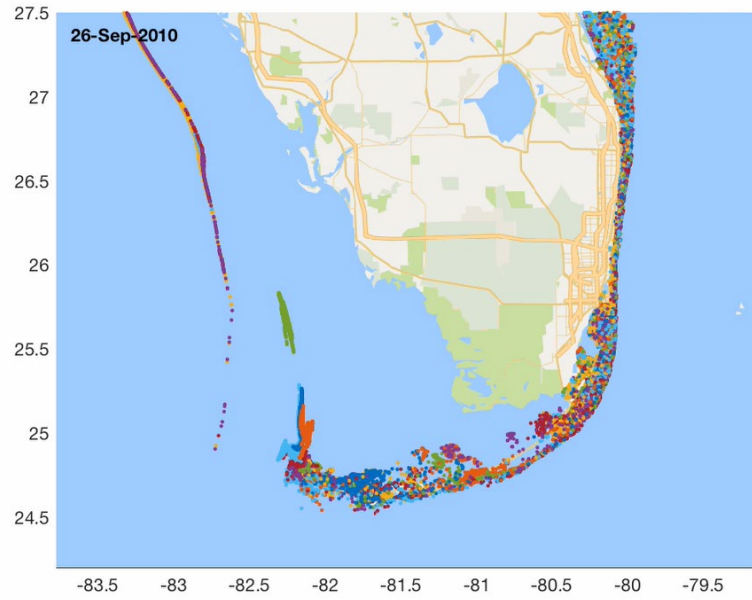
Figure 5: Last day of the dispersal simulation. Colors depict dispersal kernels from each reef.
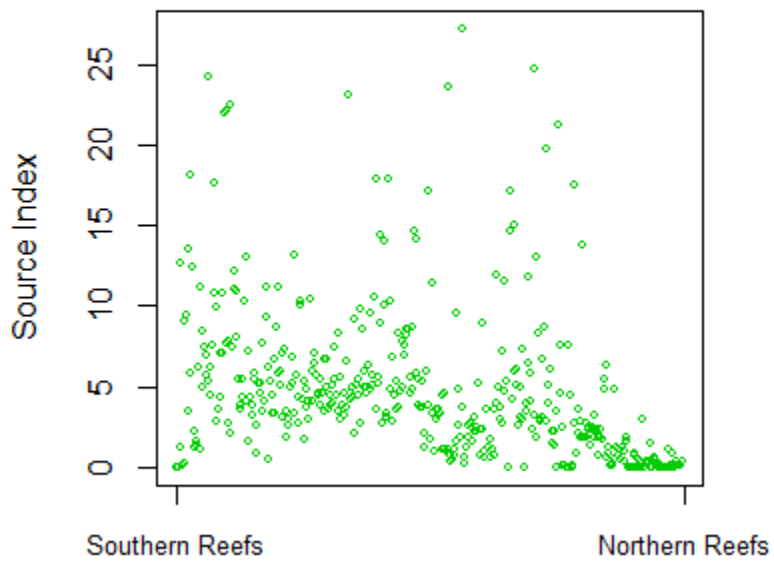
Figure 6: Source indexes for Historic *Acropora* reefs. A value of 0 means the reef did not send larvae to any reefs, whereas higher values meant the reef sent larvae to more reefs and had a higher level of output.
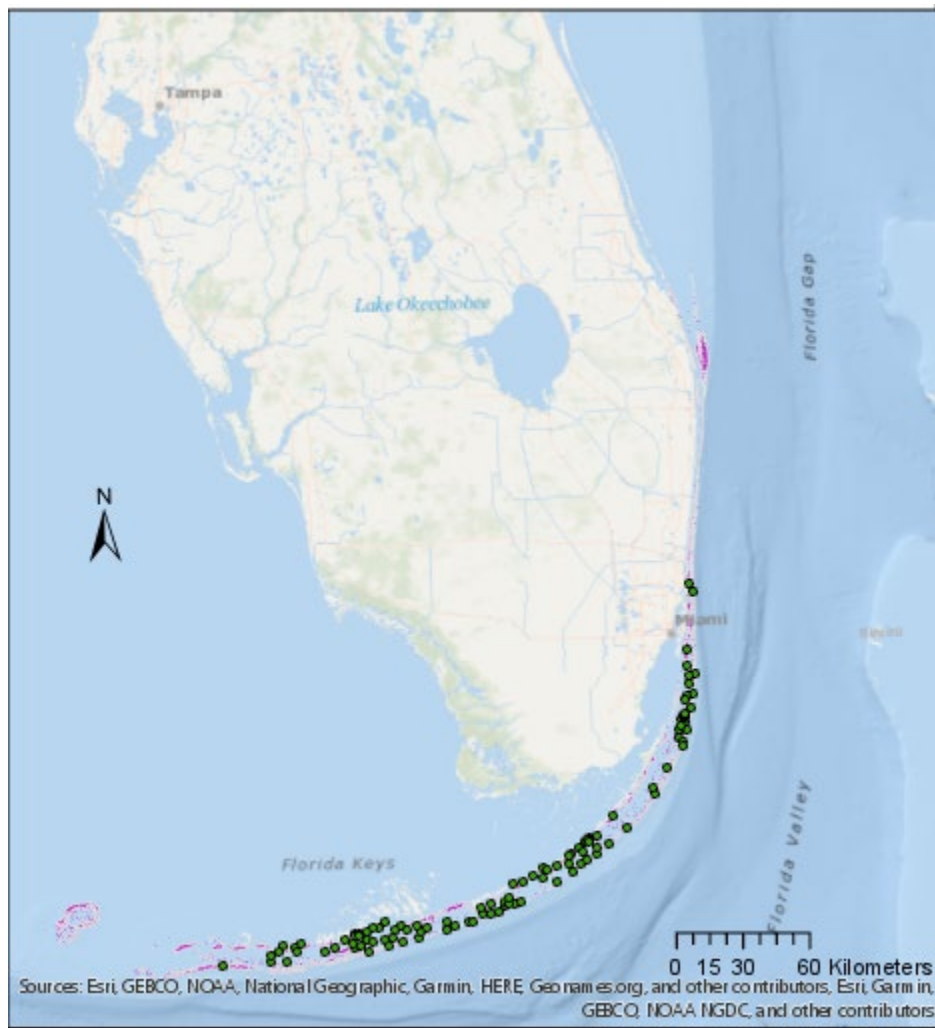
Figure 7: Historic *Acropora* Habitat source sites. Each dot represents a reef identified as a strong source. The pink coloration depicts the 95% *Acropora* Habitat from Wirt et al 2015
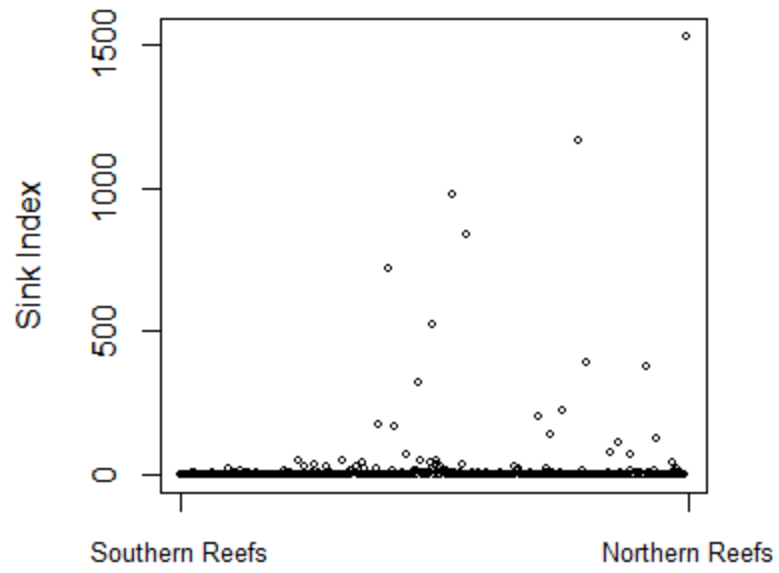
Figure 8: Sink indexes for Historic *Acropora* sites.
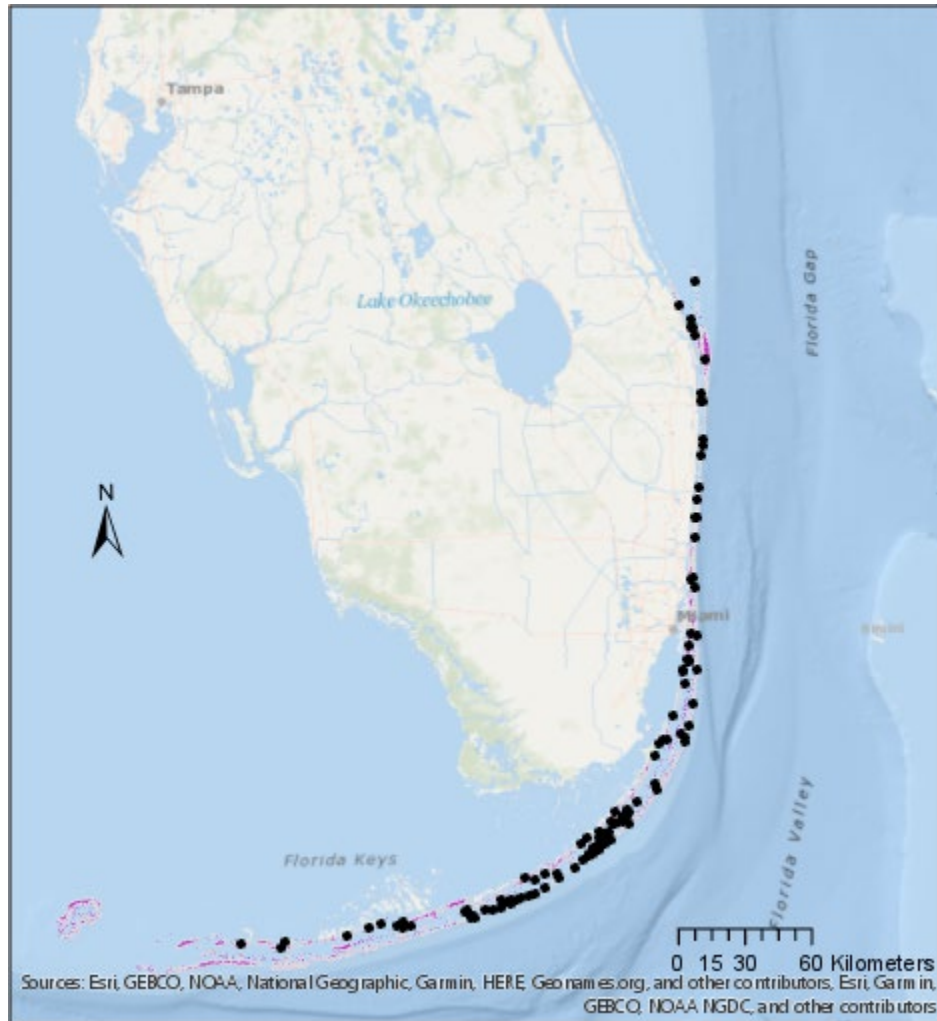
Figure 9: Sites identified as sinks from the Historic *Acropora* Connectivity Matrix
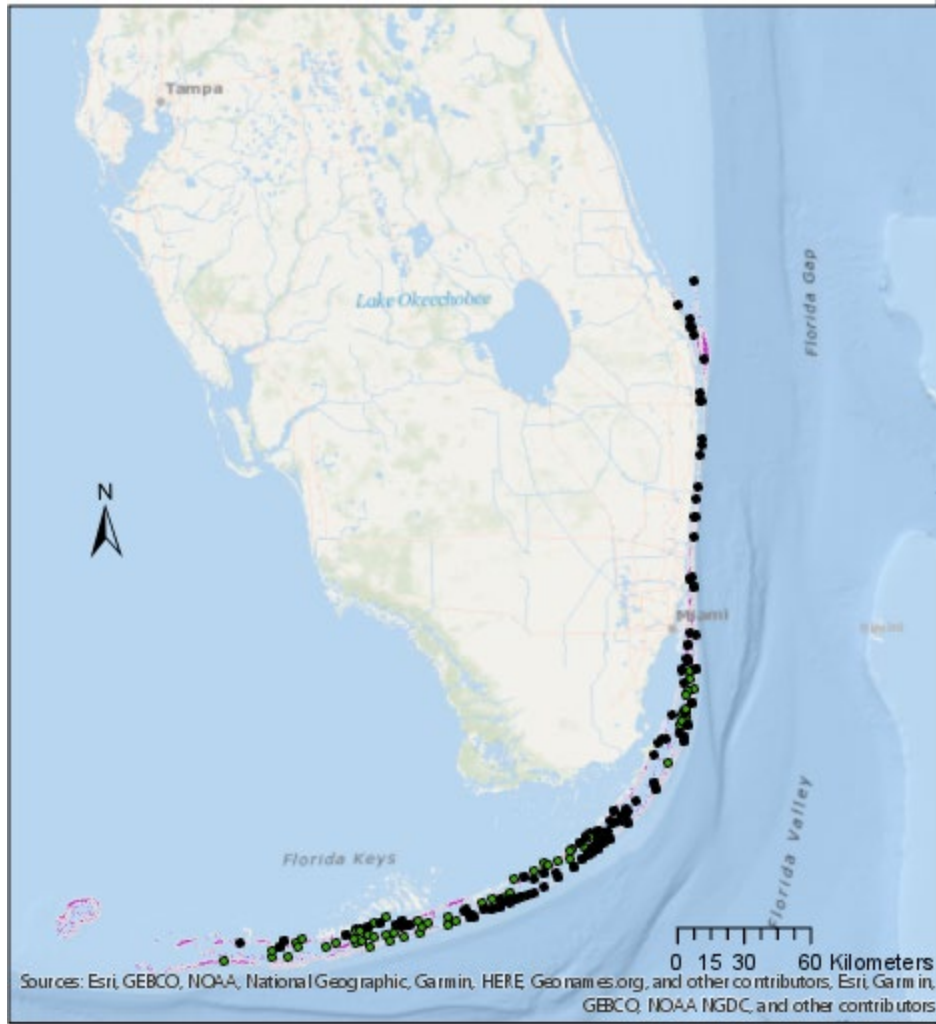
Figure 10: Sources (green) and sinks (black) from the Historic *Acropora* Connectivity Matrix

The analysis of the proportion of larvae settling indicated that, of the larvae released from the reefs, very little of it settles back onto the FRT. Therefore, most larvae are lost from the system (Figure 12). Local retention and self-recruitment occur along the entire FRT, with one fifth of historic *Acropora* reefs experience local retention and self-recruitment. However, these processes are most prevalent in the Upper Keys (Figure 13, 14, 15). There are even some reefs which are unable to transport any larvae, as all larvae are locally retained (Figure 13).
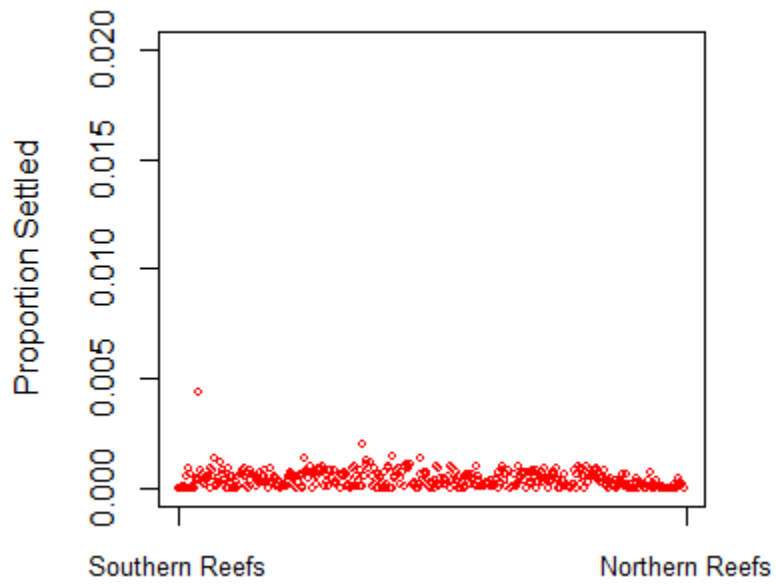
Figure 11: Settlement index for both matrixes. A value of 0 meant the reef did not have any larvae settle elsewhere.
Note that the y axis ends at 0.02, not 1
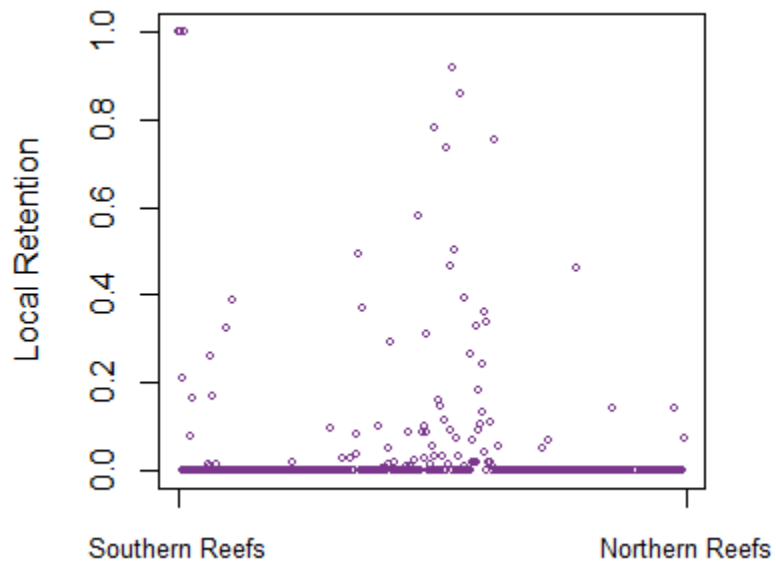
Figure 12: Local retention index. Approximately 20% of reefs had some level of local retention
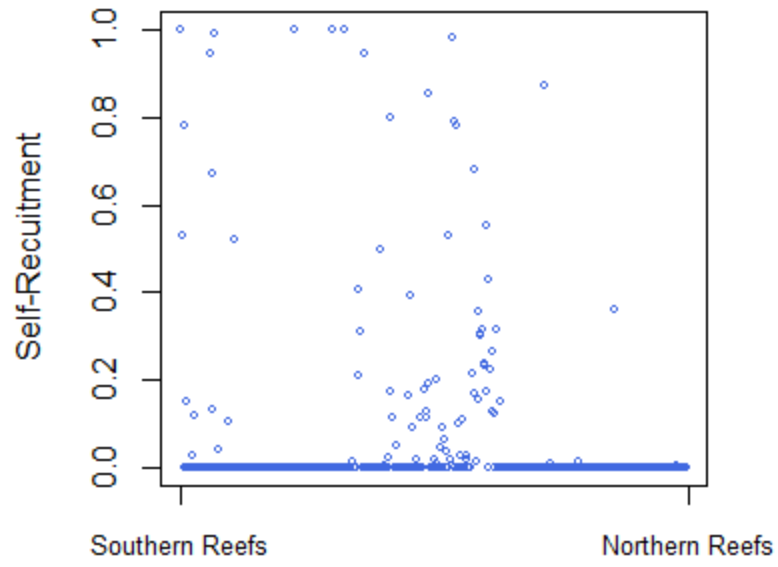
Figure 13: Self-recruitment index for historic *Acropora* sites. Reefs that experience self-recruitment were the same as those that experienced local retention.
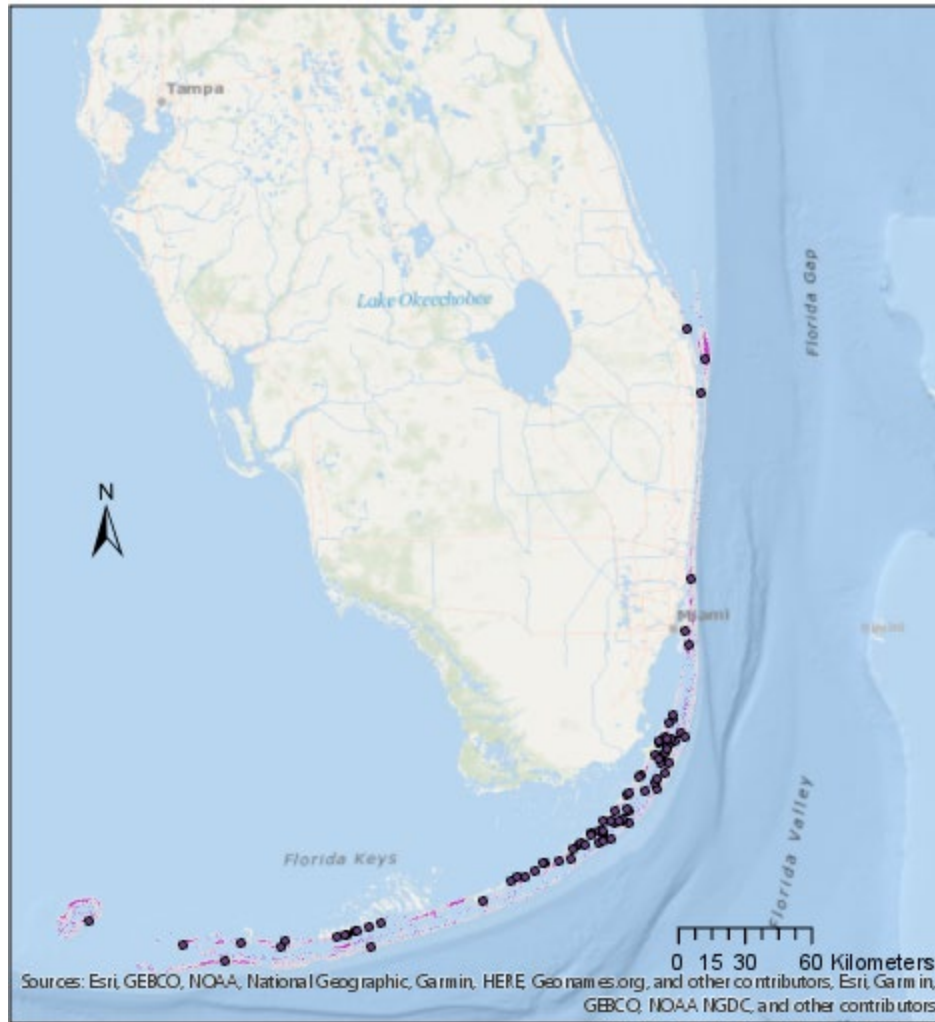
Figure 14: Historic *Acropora* sites with local retention and self-recruitment

3. *Acropora cervicornis Restoration Simulations*

3.1 Site to Site comparison

When a site without coral was outplanted, there was a noticeable change in recovery of the system relative to the baseline model, especially if that reef had a high source index. Reef A had a source index of 8.86, and reef B had a source index of 3.53, and Reef C had a source index of 13.98. In poor environmental conditions (R=0.014), outplanting at either of the three reefs decreased the recovery time equivalently, however reef C provided a greater increase in the mean percent cover of the entire FRT than occurred by restoring the other two reefs (Figures 15 and 16, Table 6). In improved conditions (increased growth (R=0.3435, 0.835), there was no

improvement from the baseline model that occurred through the restoration of a single reef. The model results were not sensitive to the initial area outplanted, and at 200m^2 the relative results were the same.

Table 5: Three reefs outplanted assuming poor environmental conditions (R=0.014). Relative increase in recovery and relative increase in Mean FRT percent cover are reported as relative improvements from the baseline current spawning model. In good and pristine environmental conditions, recovery was equivalent to the baseline model.

Outplant Scenario:	Reef A	Reef B	Reef C
Relative increase in recovery	6.67%	6.67%	6.67%
Relative increase in Mean FRT Percent Cover	0.22%	0.25%	5.00%
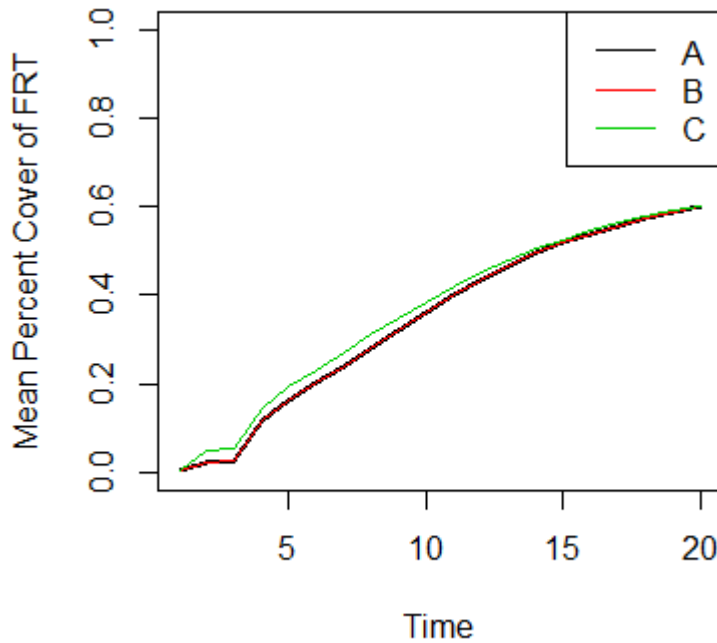
Figure 15: Mean percent cover in the entire FRT over time from the three outplanting scenarios in poor environmental conditions (low growth rate)
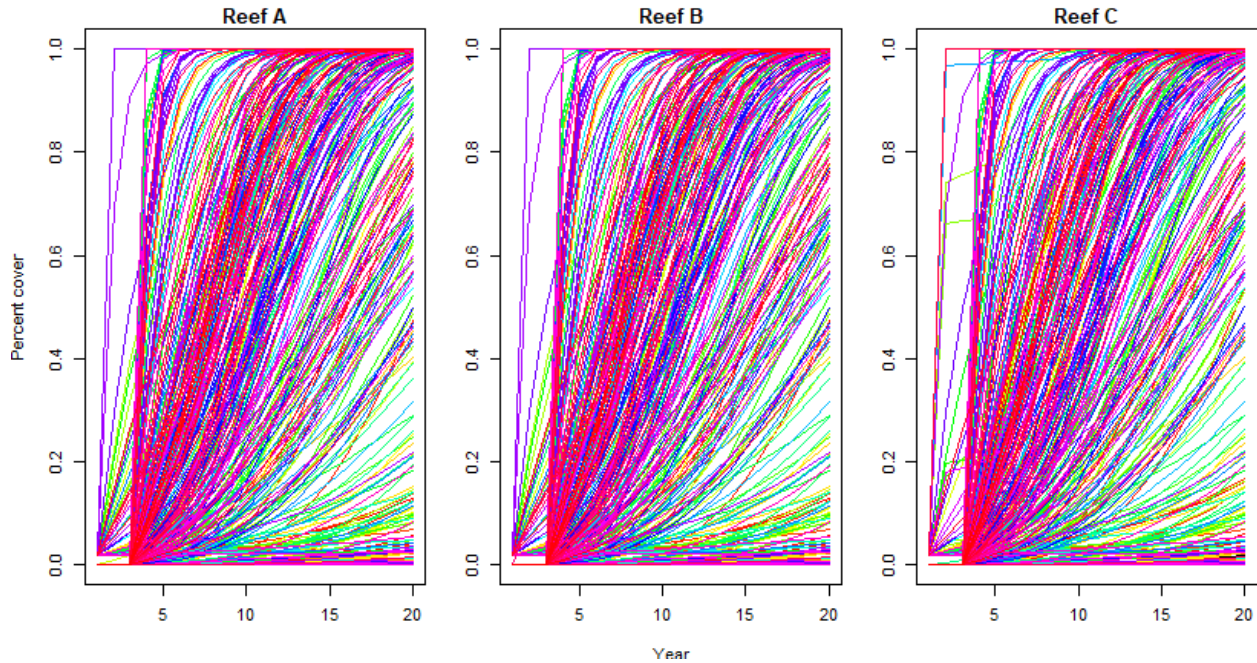
Figure 16: Change in percent cover of each Historic *Acropora* reef site in each outplanted reef scenario in poor environmental conditions. Each colored line represents a different Historic *Acropora* reef.

3.2. Restoration Spatial Scaling

The two regions randomly used for the spatial scaling comparison differed in their capacities to export larvae; such that, when the source index for each reef used in the region were added together, those in Region 1 totaled 89.87 (mean=5.99), while region 2 totaled 57.49 (mean=3.83). It was more beneficial to consolidate outplant at many reefs, rather than focusing on a few strong sources (Table 9, Figure 17). This was even more important in region 2, where outplanting on many reefs had a much stronger effect than planting heavily on a few, and even improved the recovery of the FRT (Table 10, Figure 18). Overall, outplanting in the second region provided a greater improvement to the FRT then outplanting in Region 1 (Figure 19). These results held through at the lower initial outplanting cover.

Table 6: Recovery indexes for both outplanting scenarios in each environmental condition for Region one which had a high source index relative to Region 2. No change in recovery time occurred relative to the baseline model, but each scenario led to an increase in the percent cover of the entire FRT relative to the current spawning model.

Region 1: High Source Index						
Environmental Condition:	Poor		Good		Very Good	
Outplant Scenario:	Many reefs	Few reefs	Many reefs	Few reefs	Many reefs	Few reefs
Relative increase in Recovery	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Relative increase in mean FRT Percent Cover	0.45%	0.30%	1.01%	0.89%	0.85%	0.60%
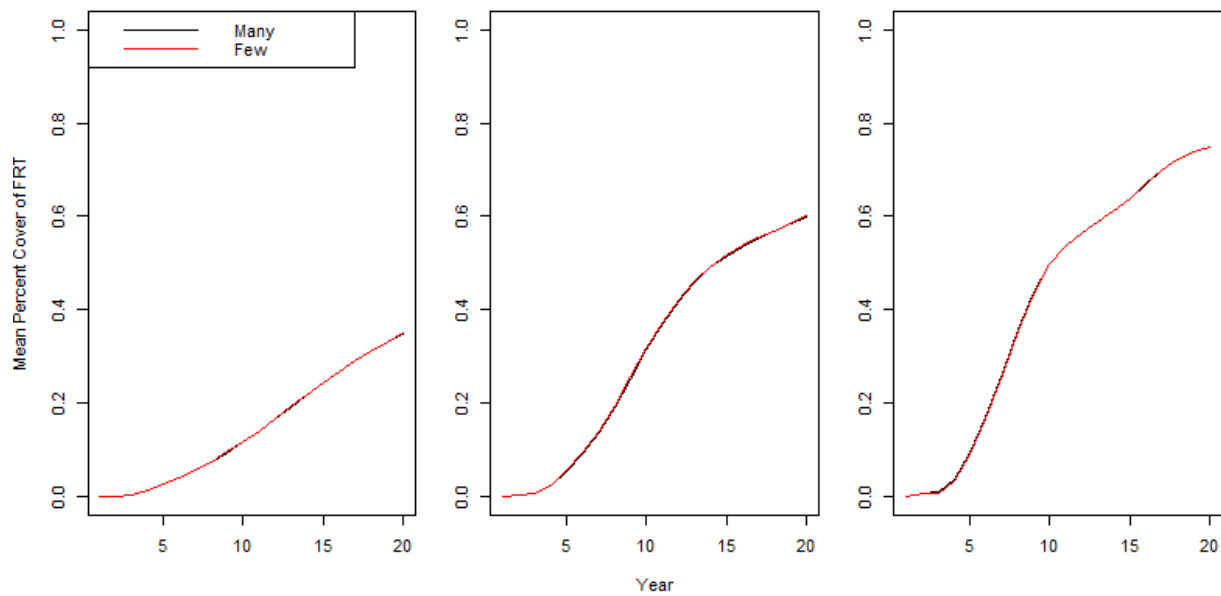
Figure 17: Region 1 simulation change in mean percent cover of FRT over time for all three environmental conditions

Table 7: Recovery indexes for both outplanting scenarios in each environmental condition for Region 2 which had a lower source index. Recovery time improved by up to 15% when many reefs were outplanted on, but both scenarios improved the mean percent cover of the FRT

Region 2: Low Source Index						
Environmental Condition:	Poor		Good		Very Good	
Outplant Scenario:	Many reefs	Few reefs	Many reefs	Few reefs	Many reefs	Few reefs
Relative increase in Recovery Time	6.67%	0	11.11%	0	14.3%	0
Relative increase in mean FRT Percent Cover	4.89%	0.35%	5.01%	2.51%	3.18%	1.75%
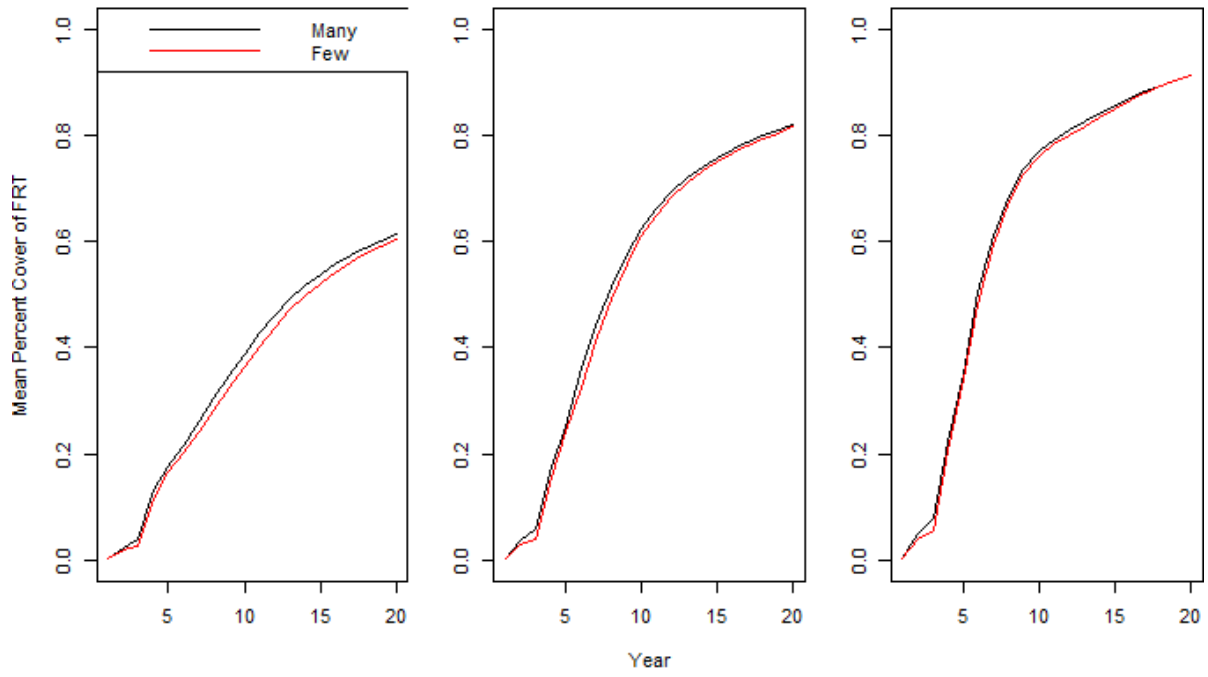
Figure 18: Region 2 simulation mean change in percent cover for all habitat reefs over time at all three growth rates
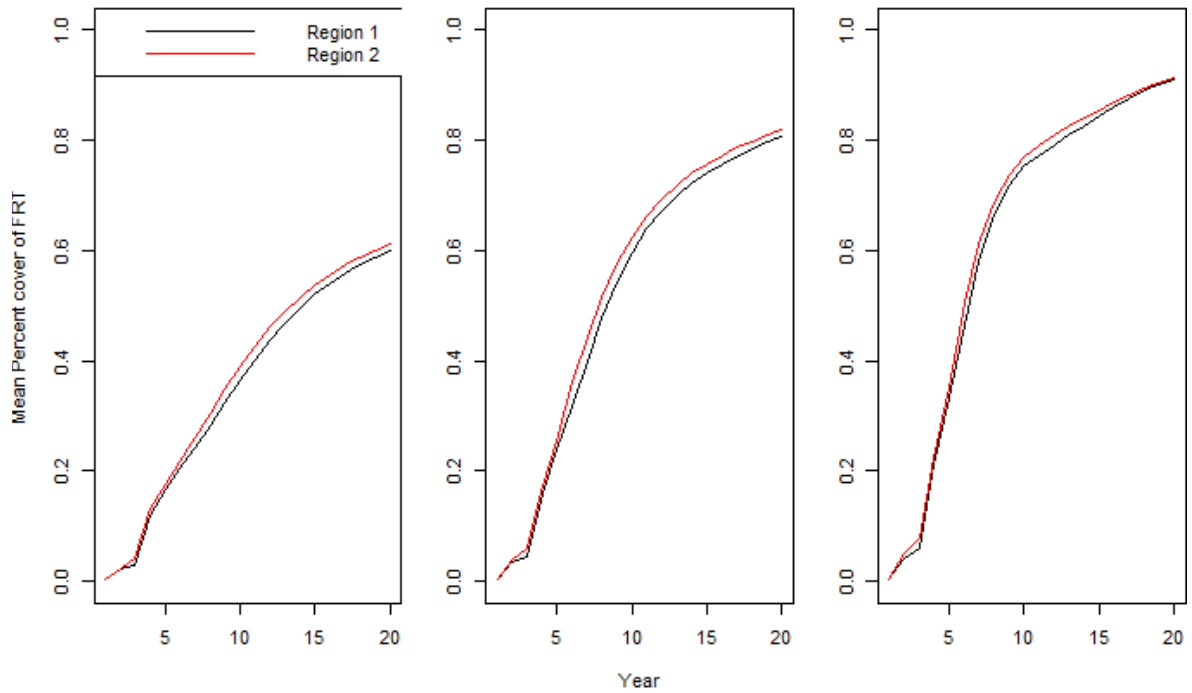
Figure 19: Many outplanting scenario compared between Region 1 and Region 2

3.3 Successive Outplanting

The simulations for successive outplanting found that spreading the outplanting effort across several years was more effective then outplanting all at once when environmental conditions are poor (i.e. when the growth rate is low). Neither scenario affected the recovery time index, but they both increased the mean percent of the FRT (Table 12, Figure 19). This was true regardless of the initial or successive outplanting quantities tested.

Table 8: Restoration indexes for the successive outplanting simulation relative to the base model

Successive vs. One-time Outplanting						
Environmental Condition:	Poor		Good		Very Good	
Outplant Scenario:	Successive	Once	Successive	Once	Successive	Once
Relative increase in recovery	0%	0%	0%	0%	0%	0%
Relative increase in mean FRT Percent Cover	0.44%	0.23%	1.21%	1.33%	1.03%	1.15%
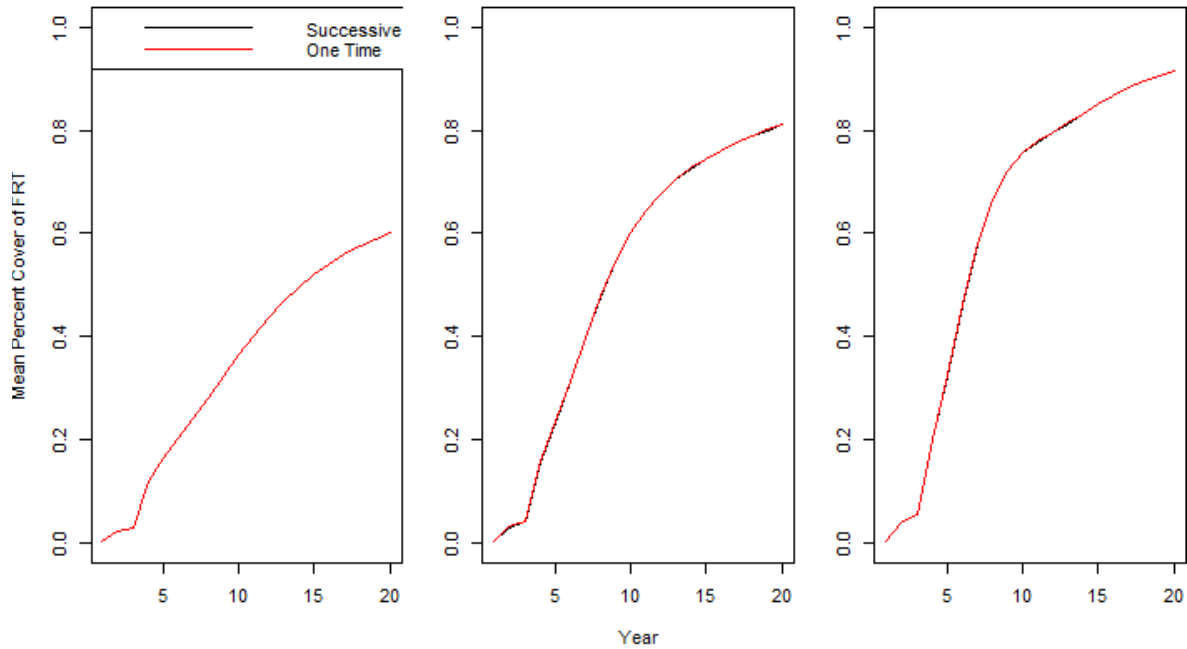
Figure 20: Mean change in percent cover on FRT overtime for successive and one-time outplanting in each environmental condition.

4. *Acropora palmata Restoration Simulations*

4.1. Site to Site comparison

For *A. palmata,* outplanting at a single reef was less effective at improving the recovery of the FRT than occurred in the *A. cervicornis* scenarios. In the current, poor conditions (low growth rate), reef E provided greater improvement of the mean cover, but in healthier reef conditions, site F was the best (Table 13, Figure 21). Despite being a source reef, reef D was not the choice in any of the conditions tested (Table 13). The model results were not sensitive to the initial area outplanted, and at 200m^2 the relative results were the same.

Table 13: Recovery indexes for the site to site scenario relative to the current spawning values to depict improvement to the FRT

Site to Site Comparison									
Environmental Condition:	Poor			Good			Very Good		
Outplant scenario:	Reef D	Reef E	Reef F	Reef D	Reef E	Reef F	Reef D	Reef E	Reef F
Relative increase in Recovery	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%	0.00%
Relative increase in mean FRT Percent Cover	0.01%	0.04%	0.01%	0.014%	0.04%	0.09%	0.02%	0.04%	0.12%
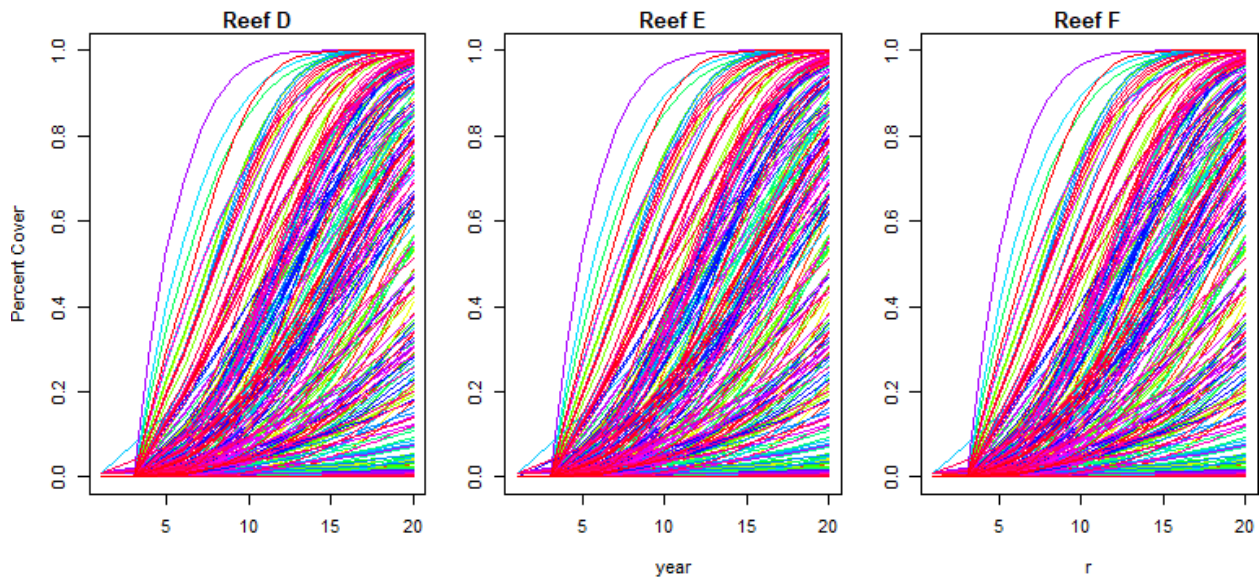
Figure 21: Comparison of Percent Cover of each reef on the FRT following the outplanting of reefs D, E, or F in poor environmental conditions. Each colored line represents a different Historic *Acropora* reef.
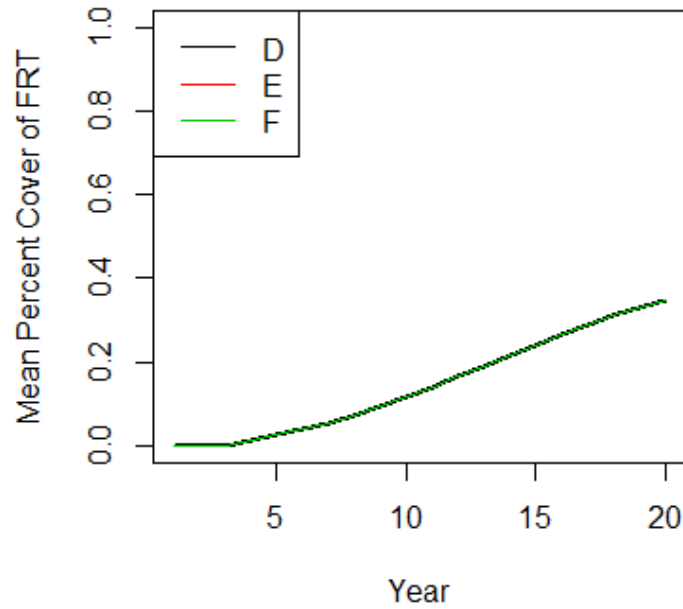
Figure 22: Change in the Mean Percent Cover of the FRT over time following outplanting at reefs D, E, and F

4.2 Spatial Scaling

For *A. palmata*, it was more beneficial to outplant at many reefs than at few reefs. As with A. cervicornis, outplanting in region 2 provided a better net benefit then Region 1.

Table 14: Restoration indexes for the region 2 simulations relative to the baseline model.

Region 1: High Source Index						
Environmental Condition:	Poor		Good		Very Good	
Outplant Scenario:	Many reefs	Few reefs	Many reefs	Few reefs	Many reefs	Few reefs
Relative increase in recovery	0	0	6.67%	6.67%	9.09%	9.09%
Relative increase in mean FRT Percent Cover	0.82%	0.55%	1.88%	2.14%	1.31%	1.08%

47

Table 15: Restoration indexes for the region 2 simulations relative to the current spawning model

Region 2: Low Source Index						
Environmental Condition:	Poor		Good		Very Good	
Outplant Scenario:	Many reefs	Few reefs	Many reefs	Few reefs	Many reefs	Few reefs
Relative increase in recovery	0	0	6.67%	6.67%	9.09%	9.09%
Relative increase in mean FRT Percent Cover	1.71%	0.75%	8.36%	5.06%	6.00%	3.53%
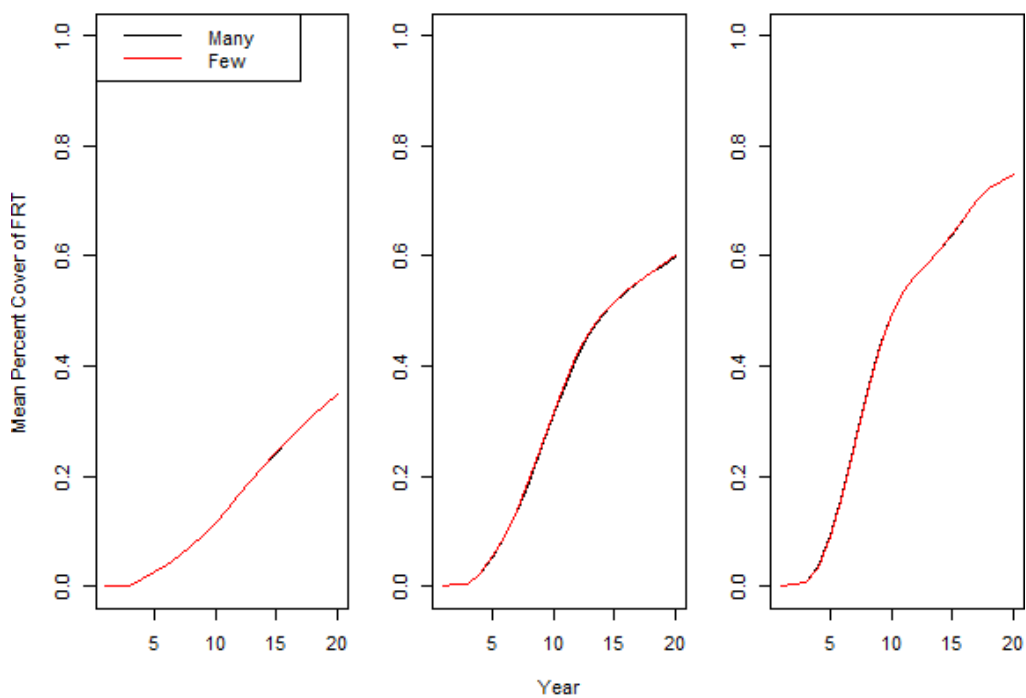
Figure 23 : Mean change in percent cover for all habitat reefs overtime for Region 1 in each environmental condition
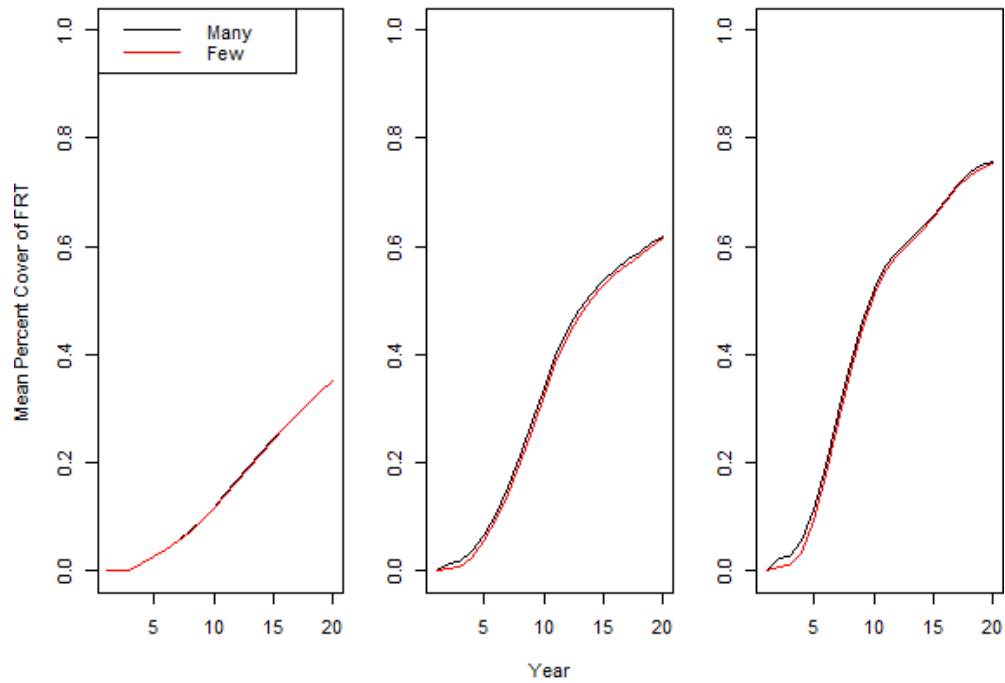
Figure 24: Mean change in percent cover for all habitat reefs overtime for region 2 in each environmental condition

Discussion

Understanding larval dispersal and population connectivity patterns in benthic organisms, such as coral, is vital for proper management of threatened species. We found a high degree of connectivity across the entire Florida Reef Tract, suggesting that restoration may be able to stimulate natural recovery. Furthermore, the high resolution of the biophysical dispersal model used in this study was able to capture higher levels of local retention than has been previously estimated for this reef system. Larvae of *Acropora* were predicted to be predominantly transported northward along the Florida Reef Tract, thus most source reefs are located in the southern part of the reef tract and sinks in the northern part. The success provided by restoring sites with a strong source index and the spatial scaling of restoration projects varied regionally due to differences in connectivity and existing coral cover. However, outplanting the same site successively was only advantageous when environmental conditions were poor, which is likely the current case on the reef. Finally, differences in population patchiness between the two species, drives the need for different approaches to their management plans.

This study showed that *Acropora* exhibit pronounced potential connectivity over a large spatial scale, but that most larvae are lost, dispersing away from the reef system. The model predicts that larvae are exchanged between all regions, but in general there were more sources in the southern end of the reef tract, while the northern end had a higher occurrence of sinks. Reefs in the Middle and Upper Keys often constituted both good sources and good sinks, constituting important "steppingstones" in connectivity. The Lower Keys were identified as the region with the greatest levels of larval exchange, which is in agreement with genetic studies that found it to have a greater genetic diversity over its small spatial scale, than across all the Cayman Islands (Drury et al. 2017). High levels of connectivity across the FRT are corroborated by genetic studies, but these studies differ in their distinctions of population structuring within the reef tract (Hemond and Vollmer 2010, Drury et al. 2017, Drury et al. 2018, Drury et al. 2019). Unlike our study which suggested similarities northward from the Middle Keys, genetic studies suggest that the Broward and Middle Keys populations are genetically distinct from the rest of the FRT (Drury et al. 2017). Furthermore, our bio-physical dispersal model predicts that most of the larvae produced in the Dry Tortugas are swept into the Gulf of Mexico or maintained through local retention processes, whereas genetically, the Dry Tortugas has been shown to be similar to all populations on the FRT (Drury et al. 2018). Caution should be used when comparing demographic connectivity with genetic connectivity, as the results of the latter can be more indicative of generations of historic population exchange (Drury et al. 2018). However, it is also plausible that the FRT acts as a sink from another region, such as Belize, because other corals species have found the Dry Tortugas population to more similar to Belize, despite its similarity to populations in the FRT (Studvian and Voss 2018). Further, our connectivity was determined from 2010 hydrodynamic data, which may or may not be representative of mean currents. Regardless, the existing high genetic diversity, especially within a patch, strongly suggest that unlike previously thought, fragmentation is not the only way these species are reproducing, and sexual recruitment must influence thicket development to some degree and investigating more sources of recruits is important.

Potential regional differences in genetic population structure reiterate the necessity of utilizing high resolution models calibrated with long term larval survival and competency dynamics; ensuring local processes are captured and the degree of distanced connections is attenuated. Such considerations are particularly important in *Acropora* which have longer pre-

competency periods than most corals and have the capacity to maintain competency for extensive periods of time (Thomas and Figueiredo et al., in preparation). As such, low resolution models are more susceptible to overestimating long-distance larval dispersal. Despite being able to disperse long distance, the 100m resolution model used in this study captured local retention and self-recruitment across all regions of the FRT, with 20% of the reefs retaining some of their larvae to some degree. It is important to consider local retention when designing management plans due to its vital role in population maintenance. When the degree of openness in systems are overestimated, it can lead to mismanagement (Cowen et al. 2000). Ecologically, local retention is important because distant dispersal can act as a barrier to successful recruitment due to phenotype-environment mismatch (Marshall et al. 2010, Weese et al. 2010). Self-recruitment also allows for increased local adaptation and acclimation within a community (Strathmann et al. 2002). However, *Acropora*, which tend to have lower rates of local retention than other corals (Figueiredo et al. 2013), have the evolutionary trade-off of faster growth allowing them to be strong competitors against species who may settle more frequently on their natal reefs (Stimson 1985). Conversely, reefs that rely solely upon growth, fragmentation, and self-recruitment, are more vulnerable to disturbances, and can have lower genetic diversity; reducing the populations' capacity to cope with environmental changes (Baums et al. 2006). Furthermore, connectivity is vital for replenishment of disturbed reefs, where even a seemingly negligible supply of larvae can lead to much quicker recovery in the absence of chronic anthropogenic stressors (Gilmour et al. 2013). For instance, the protection enacted in the Dry Tortugas is most likely vital to that population, since it likely receives little to no input from other Florida populations, and possibly relies solely on local retention processes for recruitment, if other Caribbean regions do not act as a source as we have hypothesized. Thus, areas with higher levels of local retention should be the focus of protection plans.

For connectivity considerations to be useful to management, ecological and biological processes need to be considered besides larval dispersal. Part of the discrepancy that occurs between genetic population structure and larval dispersal, may be due to pre- and post-dispersal processes (Drury et al. 2019). Metapopulation models are useful because they can include these parameters, thereby providing more ecologically meaningful results. The exclusion of these processes and relying only on larval dispersal models, would mean that only sites which had the greatest capacity to disperse larvae would be considered for restoration, which based on our

simulations with the metapopulation model, is not inherently true. We found regional variation in the type of site that is best for outplanting. In regions, such as the Lower Keys, where the population is less patchy and has high intra-regional exchange, the sites with a strong source index provided the greatest benefit for recovery for the entire FRT population. However, in regions with highly patchy populations that without restoration would otherwise have minimal exchange, it was more valuable to restore sites that replenish more impoverished reefs, rather than the sites which seeded the greatest number of reefs. In essence, poorly connected areas rely on the restoration of sites which provide a stronger rescue effect, i.e. reefs that have the ability to populate impoverished reefs (Brown and Kodric-Brown 1977). Additionally, because the source index is determined by a reef's sourcing capacity based on the sites' hydrodynamics and considers no other factors such as the health or conditions of the site, it may lack applicability to field restoration. In this way, using the metapopulation model to compare sites already established as good candidates for outplanting, will allow for the selection of the best-connected site.

Variation between regions also played an integral role in determining the spatial scaling of outplant projects for both species. We found that in areas, such as the Lower Keys, despite having a higher larval output, it was slightly more beneficial to spread outplants across many reefs. However, in the Upper Keys, which had weaker capacity to act a source, it was highly effective to spread the outplant effort across more sites. Thus, at a regional scale, within areas of poor connectivity, it is important to outplant in a manner that will facilitate the replenishment of as many barren and poorly connected reefs as possible. To date, these results have not been validated in the field, as few restoration studies incorporate ecological processes, such as recruitment and spawning following outplanting (Ladd et al. 2018). Furthermore, research in spatial scaling thus far as only looked outplanting density and spatial planning within a site, not amongst sites (Griffin et al. 2015, Goergen and Gilliam 2018). Considering how depauperate the populations have become; it is vital to address questions regarding methodologies for reestablishing spatially connected populations in a manner that promotes natural recovery and genotypic diversity (Lirman and Shopmeyer 2016). Ecological modeling can provide good suggestions to design experimental trials to answer these questions.

Temporally staggering outplanting effort was found to be optimal when environmental conditions were poor, even though it was assumed successive outplants had similarly poor survival. However, some research suggests that successively outplanting a site will increase the survival of new outplants over the primary ones (Rinkevich 2018). The potential increase in survival and growth provided by successive outplanting, could allow the model to predict a greater difference in benefit to successively outplant, especially if the environmental conditions are poor. But, when growth and survival are good, due to environmentally favorable conditions, staggering outplanting effort over time is unnecessary. Current growth rates of *Acropora* are already estimated to be diminished, but as atmospheric CO_2 continues to rise, it is much more likely that in the future there will be net negative population growth. Increasing atmospheric CO_2 in the atmosphere is predicted to cause reefs to experience mass bleaching annually within the next twenty years (Hoegh-Guldberg et al. 2017) resulting in not only mass mortality, but also reducing the energy reserves of surviving corals otherwise allocated to growth and reproduction. While large scale action is needed to prevent climate change, in the meantime temporally varying outplanting effort will help to optimize restoration effort and increase survival.

Despite their very similar life history traits, there are distinct differences in the current population distribution of *Acropora cervicornis* and *Acropora palmata* that require differing management plans. The greater population patchiness and mean cover on the FRT of *A. palmata* means it requires greater levels of outplanting, and more consideration should be used in spatial and temporal planning. Thus, it is even more important to include all aspects of recovery by using metapopulation modeling when assessing *A. palmata*, since their potential connectivity is similar to *A. cervicornis*. Currently, there is greater focus by restoration projects on *A. cervicornis* in Florida, despite the declines in both species, which has had documented success (Miller et al. 2016)

While the metapopulation model developed in this study can be a useful tool to for making relative comparisons to make informed restoration decisions, it is a simplistic model which is limited in its capacity to simulate the true ecological dynamics of the population. The model, as it exists does not allow for a net negative population growth, which is perhaps more realistic with the declines in live tissue cover that are being seen (Williams et al. 2008, Miller et al. 2016, Goergen and Gilliam 2018). However, in the future, this could be addressed by forcing

disturbances into the model. Currently only the hydrodynamics from the year 2010 have been considered, so more years need to be included to fully encompass regional trends in connectivity and the stochastic nature of successful recruitment. Finally, the study should ideally be expanded to look at connectivity across the entire Caribbean to determine how closed of a system the FRT is in respect to the broader region.

Despite the inherent limitations of modelling-based projects, this study helped to fulfill restoration management needs by incorporating considerations of sexual reproduction and connectivity into the decision-making process. The maintenance of the genetic diversity of Floridian *Acropora*, and the successful re-establishment of the population in an economically feasible way depends on utilizing the natural recovery processes of the corals in conjunction with lessening of chronic anthropogenic stressors.

Literature Cited

Albright, R., Mason, B., Miller, M., & Lagdon, C. (2010). Ocean Acidificaiton compromises recruitment success of the threatened Caribbean coral *Acropora palmata*. *PNAS, 107*(47), 20400-20400.

Arias, A., Cinner, J. E., Jones, R. E., & Pressey, R. L. (2015). Levels and drivers of fishers' compliance with marine protected areas. *Ecology and Society, 20*(4).

Aronson, R. B., & Precht, W. F. (2001). White-band disease and the changing face of Caribbean coral reefs. *Hydrobiologia, 460*, 25-38.

Attributing mortality among drivers of population decline of *Acropora palmata* in the Florida Keys (USA). (2012). *Coral Reefs, 31*, 369-382.

Babcock, R. C., Baird, A. H., Piromvaragorn, S., Thomson, D. P., & Willis, B. L. (2003). Identification of scleractinian coral recruits from the Indo-Pacific Reef. *Zoological Studies, 42*(1), 211-226.

Bak, R., & Engel, M. (1979). Distribution, abundance, and survival of juvenile hermatypic corals and the importance of life history strategies in the parental coral community. *Marine Biology, 54*, 341-352.

Baums, I. (2008). A restoration genetics guide for coral reef conservation. *Molecular Ecology, 17*(12), 2796-2811.

Baums, I. B. (2005). Regionally isolated populations of an imperiled Caribbean coral, *Acropora palmata*. *Molecular Ecology*, 1377-1390.

Baums, I. B., Miller, M. W., & Hellberg, M. E. (2006). Geographic variation in clonal structure in a reef building caribbean coral, *Acropora palmata*. *Ecological Monographs, 76*(4), 503-519.

Brown, J. H., & Kodric-Brown, A. (1977). Turnover Rates in Insular Biogeography: Effect of Immigration on Extinction. *Ecology, 58*(2), 445-449.

Burgess, S., Nikols, K., Griesmer, C., Barnett, L., Dedrick, A., Satterthwaite, E., . . . Botsford, L. (2014). Beyond Connectivity: how empirical methods can quantify population persistence to improve marine protected area design. *Ecological Applications, 24*(2), 257-270.

Cesar, H., Burke, L., & Pet-Soede, L. (n.d.). *The economics of worldwide coral reef degradation* (3rd ed.). Cesar Environmental Economics Consulting.

Chamberland, V. F., Petersen, D., Latjinhouwers, K. R., Snowden, S., Mueller, B., & Vermeij, M. J. (2016). Four-year-old Caribbean *Acropora* colonies reared from field-collected gametes are sexually mature. *Bull Mar Sci, 92*(2), 000-000.216.

Chamberland, V. F., Vermeij, M. J., Brittsan, M., Carl, M., Schick, M., Snowden, S., . . . Petersen, D. (2015). Restoration of critically endangered elkhorn coral (*Acropora palmata*) populations using larvae reared from wild-caught gametes. *Global Ecology and Conservation, 4*, 526-537.

Connolly, S. R., & Baird, A. H. (2010). Estimating dispersal potential for marine larvae: dynamic models applied to scleractinian corals. *Ecological Society of America, 91*(12), 3572-3583.

Cowen, R. K., Lwiza, K. M., Sponaugle, S., Paris, C. B., & Olson, D. B. (2000). Connectivity of Marine Populations: Opened or Closed? *Science, 287*.

Cowen, R. K., Paris, C. B., & Srinivasan, A. (2006). Scaling of connectivity in marine populations. *Science, 311*.

Drury, C., & Lirman, D. (2017). Making biodiversity work for coral reef restoration. *Biodiversity, 18*(1), 23-25.

Drury, C., Greer, J. B., Baums, I., Gintert, B., & Lirman, D. (2019). Clonal diversity impacts coral cover in *Acropora cervicornis* thickets: Potential relationships between density, growth, and polymorphisms. *Ecology and Evolution*, 1-14.

Drury, C., Paris, C. B., Kourafalou, V. H., & Lirman, D. (2018). Dispersal capacity and genetic relatedness in *Acropora cervicornis* on the Florida Reef Tract. *Coral Reefs, 37*, 585-596.

Drury, C., Schopmeyer, S., Goergen, E., Bartels, E., Nedimyer, K., Johnson, M., . . . Lirman, D. (2017). Genomic patterns in *Acropora cervicornis* show extensive population structure and variable genetic diversity. *Ecology and Evolution*, 6188-6199.

Edwards, A. (2010). Reef Rehabilitation Manual.

Epstein, N., Bak, R. P., & Rinkevich, B. (2001). Strategies for gardening denuded coral reef areas: the applicability of using different types of coral material for reef restoration. *Restoration Ecology, 9*(4), 432-442.

Ferrario , F., Beck, M., Storlazzi, C., Micheli, F., Shepard, C., & Airoldi, L. (2013). The effectiveness of coral reefs for coastal hazard risk reduction and adaptation. *Nature Communications*.

Figueiredo, J., Baird, A. H., & Connolly, S. R. (2013). Synthesiszing larval confidence dynamics and reef scale retention reveals a high potential for self recruitment in corals. *Ecology, 94*(3), 650-659.

Figueiredo, J., Baird, A., Harii, S., & Connolly, S. (2014). Increased local retention of reef coral larvae as a result of ocean warming. *Nature Climate Change, 4*.

Foster, A. (1980). Enviornmental variation of skeletal morphology within the caribbean reef corals Montastrea annularis and Siderastrea siderea. *Bulletin of Marine Science, 30*(3), 678-709.

Frys, C., Le Henaff, M., Figueiredo, J., Kuba, A., Walker, B., Lambrechts, J., . . . Hanert, E. (2017). High-Resolution marine connectivity modelling in the Florida Reef Tract.

Gaggiotti, O. E. (2017). Metapopulations of marine species with larval dispersal: A counterpoint to Ilkka's Glanville fritillary metapopulations. *Ann. Zool. Fennici*, 97-112.

Galindo, H. M., Olson, D. B., & Palumbi, S. R. (2006). Seascape Genetics: A coupled oceanographic-genetic model predicts population structure of Caribbean corals. *Current Biology, 16*, 1622-1626.

Gardner, T. A., Cote, I. M., Gill, J. A., Grant, A., & Watkinson, A. R. (2005). Hurricanes and Caribbean Coral Reefs: Impacts, Recovery Patterns, and Role in Long-Term Decline. *Ecology, 86*(1), 174-184.

Gilmour, J., Smith, L., Heyward, A., Baird, A., & Pratchett, M. (2013). Recovery of an isolated coral reef system following severe disturbance. *Science, 340*(69).

Ginsburg, R., Gischler, E., & Kiene, W. (2001). Partial mortality of massive reef building corals: an index of patch reef condition, Florida Reef Tract. *Bulletin of Marine Science, 69*(3), 1149-1173.

Gladfelter, E. H., Monahan, R. K., & Gladfelter, W. B. (1978). Growth rates of five reef building corals in the Northeastern Caribbean. *Bulletin of Marine Science, 28*(4), 728-734.

Gleason, D. F., Danilowiez, B. S., & Nolan, C. J. (2009). Reef waters stimulate substratum exploration in planulae from brooding Caribbean corals. *Coral Reefs*, 549-554.

Goergen, E. A., Moulding, A. L., Walker, B. K., & Gilliam, D. S. (2019). Identifying causes of temporal changes in *Acropora cervicornis* populations and the potential for recovery. *Frontiers in Marine Science, 6*(36).

Goreau, T., & Wells, J. (1967). The shallow water scleractinia of Jamaica: revised list of speices and thier vertical distribution range. *Bulletin of Marine Science*, 442-453.

Gosselin, L. A., & Qian, P.-Y. (1997). Juvenile mortality in benthic marine invertebrates. *Marine Ecology Progress Series, 146*, 265-282.

Hall, V. R., & Hughes, T. P. (1996). Reproductive strategies of modular organisms: comparative studies of reef-building corals. *Ecology, 77*(3), 950-963.

Hellberg, M. E. (2007). Footprints on the water: the genetic wake of dispersal among coral reefs. *Coral Reefs, 26*(3), 463-473.

Hoegh-Guldberg, O., Mumby, P. J., Hooten, A. J., Steneck, R. S., Greenfield, P., Gomez, E., & Harvell, C. D. (2007). Coral Reefs under rapid climate change and ocean acidification. *Science, 318*(5857), 1737-1742.

Hoegh-Guldberg, O., Poloczanska, E. S., Skirving, W., & Dove, S. (2017). Coral reef ecosystems under climate change and ocean acidification. *frontiers in marine science, 4*(158).

Hoey, A. S., Howells, E., Johansen, J. L., Hobbs, J.-P. A., Messmer, V., McCowan, D. M., . . . Pratchett, M. S. (2016). Recent Advances in Understanding the Effects of Climate Change on Coral Reefs. *Diversity, 8*(12).

Hughes, T. P., Baird, A. H., Bellwood, D. R., Card, M., Connolly, S. R., Folke, C., . . . Roughgarden, J. (2003). Climate change, human impacts, and the resiliance of coral reefs. *Science, 309*.

Hughes, T. P., Baird, A. H., Dinsdale, E. A., Moltschaniwskyj, N. A., Pratchett, M. S., Tanner, J. E., & Willis, B. L. (2000). Supply side ecology works both ways: the link between bethic adults, fecundity, and larval recruits. *Ecology, 81*(8), 2241-2249.

Hughes, T., & Tanner, J. (2000). Recruitment failure, life history, and long term decline of Carribean corals. *Ecological Society of America, 81*(8), 2250-2263.

Hughes, T., Kerry, J., Alvarez-Noriega, M., Alvarez-Romero, J., Anderson, K., Baird, A., & Babcock, R. (2017). Global warming and recurrent mass bleaching of corals. *Nature, 543*, 373-377.

Johns, G. M. (2001). *Socioeconomic study of reefs in southeast Florida.* Report by Hazen and Sawyer under contract to Broward County, Florida.

Johnson, M. E., Lustic, C., Bartels, E., Baums, I. B., & Gilliam, D. S. (2011). Carribbean *Acropora* restoration guide: best practices for propogation and population enhancement. NSUWorks.

Jones, G. P., Almany, G. R., Russ, G. R., Sale, P. F., Steneck, R. S., Van Oppen, M. J., & Willis, B. L. (2009). Larval retention and connectivity amoung populations of corals and reef fishes: history, advances, and challenges. *Coral Reefs*, 307-325.

Kuffner, I. B., Walters, L. J., Becerro, M. A., Paul, V. J., Ritson-Williams, R., & Beach, K. S. (2006). Inhibition of coral recruitment by macroalgae and cyanobacteria. *Marine Ecological Progress Series, 323*, 107-117.

Ladd, M., Miller, M. W., Hunt, J. H., Sharp, W. C., & Burkepile, D. E. (2018). Harnessing ecological processes to facilitate coral restoration. *Front Ecol Environ, 16*(4), 239-247.

Lirman, D. (2000). Fragmentation in the branching coral *Acropora palmata*: growth, survivorship, and reproduction of colonies and fragments. *Journal of Experimental Marine Biology and Ecology, 251*, 41-57.

Lirman, D. (2001). Competition between macroalgae and corals: Effects of herbivore exclusion and increased algal biomass on corals. *Coral Reefs*.

Lirman, D., & Fong, P. (2007). Is proximity to land based sources of coral stressors an appropriate measure of risk to coral reefs? An example from the Florida Reef Tract. *Marine Pollution Bulletin, 54*, 779-791.

Lirman, D., & Schopmeyer, S. (2016). Ecological solutions to reef degradation: optimizing coral reef restoration in the Caribbean and Western Atlantic. *PeerJ*.

Lirman, D., Schopmeyer, S., Galvan, V., Drury, C., Baker, A. C., & Baums, I. B. (2014). Growth Dynamics of the Threatened Caribbean Staghorn Coral *Acropora cervicornis*: Influence of Host Genotype, Symbiont Identity, Colony Size, and Environmental Setting. *PLOS one, 9*(9).

M.W. Miller, A. S. (2002). An Analysis of the loss of Acroporid corals at Looe Key, Florida, USA: 1983-2000. *Coral Reefs*(21), 179-182.

Marshall, D. J., Monro, K., Bode, M., & Keough, M. J. (2010). Phenotype–environment mismatches reduce connecitivity in the sea. *Ecology Letters, 13*, 128-140.

Mayorga Adame, C. G., Batchelder, H. P., & Spit, Y. H. (2017). Modeling larval connectivity of coral reef organisms in the Kenyan-Tanzania region. *Frontiers in Marine Science, 4*(92).

Mercado-Molina, A. E., Ruiz-Diaz, C. P., & Sabat, A. M. (2015). Demographics and dynamics of two restored populations of the threatened reef-building coral *Acropora cervicornis. Journal of Nature Conservation, 24, 17-23.*

Mercado-Molina, A. E., Ruiz-Diaz, C. P., Perez, M. E., Rodriguez-Barreras, R., & Sabat, A. (2015). Demography of the threatened coral *Acropora cervicornis*: implications for its management and conservation. *Coral Reefs*.

Metaxas, A., & Saunders, M. (2009). Quantifying the "Bio-" Components in Biophysical Models of Larval Transport in Marine Benthic Invertebrates: Advances and Pitfalls . *Biol. Bull.*, 257-272.

Miller, M. W., Kerr, K., & Williams, D. E. (2016). Reef scale trends in Florida *Acropora* spp. abundance and the effects of population enhancement. *Peer J*.

Moberg, F., & Folke, C. (1999). Ecological goods and services of coral reef systems. *Ecological Economies, 29*, 215-233.

Nagelkerken, I., Van der Velde, G., Gorissen, M., Meijer, G., van't Hof, T., & den Hartog, C. (2000). IMportance of mangroves, seagrass beds, and the shallow coral reef as a nsery for important coral reef fishes using a cisual census technique. *Estuarine, Coastal, and Shelf Science, 51*(1), 31-44.

Nishikawa, A., Katoh, M., & Sakai, K. (2003). Larval settlement rates and gene flow of broadcast spawning (*Acropora tenuis)* and planula brooding (Stylophora pistillata) corals. *Marine Ecology Progress Series, 256*, 87-97.

Pandolfi, J. M., & Jackson, J. B. (2006). Ecological persistence interrupted in Caribbean coral reefs. *Ecology Letters*.

Randall, C. J., & van Woesik, R. (2015). Contemporary white-band disease in Caribbean corals driven by climate change. *Nature Climate Change*, 1-5.

Renegar, D. A., & Reigl, B. M. (2005). Effect of nutrient enrichment and elevated pCO2 partial pressure on growth rate of the Atlantic scleractinian coral *Acropora cervicornis*. *Marine Ecolgoy Progress Series, 293*, 69-76.

Richmond, R. H., & Hunter, C. L. (1990). Reproduction and recruitment of corals: comparisons amoung the Caribbean, the Tropical Pacific, and the Red Sea. *Marine Ecology Progress Series, 60*, 185-203.

Rinkevich, B. (2008). Management of coral reefs: We have gone wrong when neglecting active reef restoration. *Marine Pollution Bulletin, 56*, 1821-1824.

Rinkevich, B. (December, 2019). Gardening the coral reefs - reviewing two decades of activities to construct the "reefs of tomorrow". Keynote, Reef Futures.

Ritson-Williams, R., Paul, V. J., Arnold, S. N., & Steneck, R. S. (2009). Larval settlement preferences and post-settlement survival of the threatened Caribbean corals *Acropora palmata* and *A. cervicornis*. *Coral Reefs, 29*(1), 71-81.

Schopmeyer, S. A., Lirman, D., Bartels, E., Byrne, J., Gilliam, D. S., Hunt, J., . . . Walter, C. (2012). In situ coral nurseries serve as genetic repositories for coral reef restoration after an extreme cold water event. *Restoration Ecology, 20*(6), 696-703.

Selig, E., & Bruno, J. (2010). A global analysis of the effectiveness of Marine Protected Areas in preventing coral loss. *PLoS ONE*.

Smith, L. D., & Hughes, T. P. (1999). An experimental assessment of survival, re-attachment, and fecundity of coral fragments. *Journal of Experimental Marine Biology and Ecology*, 147-164.

Soong, K. (1991). Sexual reproductive patterns of shallow water reef corals in panama. *Bulletin of Marine Science, 49*(3), 832-846.

Soong, K. (1993). Colony size as a species character in massive reef corals. *Coral Reefs*, 77-83.

Soong, K., & Lang, J. C. (1992). Reproductive integration of coral reefs. *Biological Bulletin, 183*(3), 418-431.

Spalding, M. D., & Brown, B. E. (2015). Warm-water coral reefs and climate change. *Science, 650*(6262), 769-771.

Spurgeon, J. P. (192). The economic valuation of coral reefs. *Marine Pollution Bulletin, 24*(11), 529-536.

St. Gelais, A., Chaves-Fonnegra, A., Brownlee, A., Kosmynin, V., & Gilliam, D. (2016). Fecundity and sexual maturity of Siderastrea siderea at high latitude along the Florida Reef Tract, USA. *Invertebrate Biology, 135*(1), 46-57.

Strathmann, R. R., Hughes, T. P., & Kuris, A. M. (2002). Evolution of local recruitment and its consequences for marine populations. *Bulletin of Marine Science, 70*, 377-396.

Szmant, A. M. (1986). Reproductive ecology of Caribbean reef corals. *Coral Reefs, 5*, 43-54.

Szmant, A. M., & Miller, M. W. (2006). Settlement preferences and post-mortality of laboratory cultured and settled larvae of Caribbean hermatypic corals Montastrea faveolata and *Acropora palmata* in the Florida Keys, USA. *Proceedings of 10th International Coral Reef Symposium*, 13-49.

Thomas, C. B. (2015). Connectivity between submerged and near sea-surface coral reefs: Can submerged reef populations act as refuges? *Diversity and Distributions*.

Treml, E. A., Roberts, J. J., Chao, Y., Halpin, P. N., Possingham, H. P., & Riginos, C. (2012). Reproductive output and duration of the Pelagic Larval Stage Determine Seascape- Wide Connectivity of Marine Populations. *Integrative and Comparative Biology, 52*(4), 525-537.

Vargas-Angel, B., Colley, B. S., Hoke, S. M., & Thomas, D. J. (2005). The reproductive seasonality and gametogenic cycle of *Acropora cervicornis* off Broward County, Florida, USA. *Coral Reefs*.

Vargas-Angel, B., Thomas, J. D., & Hoke, S. M. (2003). High Latitude of *Acropora cervicornis* thickets off Fort Lauderdale, Florida, USA. *Coral Reefs*, 465-473.

Vermeij, M., Marhaver, K., Huijbers, C., Nagelkerken, I., & Simpson, S. (2010). Coral larvae move toward reef sounds. *PLoS ONE*.

Walker, B. K., Larson, E. A., Moulding, A. L., & Gilliam, D. S. (2012). Small scale mapping of indeterminate aborescent acroporid coral (*Acropora cervicornis*) patches. *Coral Reefs, 31*, 885-894.

Wallace, C. C. (1985). Reproduction, recruitment, and fragmentation in nine sympatric species of the coral genus *Acropora*. *Marine Biology*, 217-233.

Weese, D. J., Shwartz, A. K., & Bentzen, P. (2010). Eco-evolutionary effects on population recovery following catastrophic disturbance. *Evolutionary Applications*, 354-366.

Williams, D. E. (2012). Attributing mortality among drivers of population decline in *Acropora Cervicornis* in the Florida Keys (USA). *Coral Reefs, 31*, 369-382.

Williams, D. E., & Miller, M. (2011). Attributing mortality among drivers of population decline in *Acropora palmata* in the Florida Keys (USA). *Coral Reefs*.

Williams, D. E., Miller, M. W., & Kramer, K. L. (2008). Recruitment failure in Florida species *Acropora palmata*, a threatened Caribbean coral. *Coral Reefs*, 697-705.

Wirt, K. E., Hallock, P., Palandro, D., & Lunz, K. S. (2015). Potential Habitat of   spp. on reefs of Florida, Puerto Rico, and the US Virgin Islands. *Global Ecology and Conservation*, 242-255.

Wittenberg, M., & Hunte, W. (1992). Effects of eutrophication and sedimentation on juvenile corals. *Marine Biology, 112*(1), 131-138.

Wood, S., Paris, C. B., Ridgwell, A., & Hendy, E. J. (2014). Modelling dispersal and connectivity of broadcast spawning corals at the global scale. *Global ecology and biogeography, 23*, 1-11.

Young, C. N., Shopmeyer, S., & Lirman, D. (2012). A review of reef restoration and coral propagation using the threatened genus A*cropora* in the caribbean and western atlantic. *Bulletin of Marine Science, 88*(4), 1075-1098.