NEGLIGIBLE EFFECT OF DENSITY ON CORAL SURVIVORSHIP AND IMPLICATIONS FOR REEF RESTORATION

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I certify that I have read this thesis and that, in my opinion, it is satisfactory in scope and quality as a thesis for the degree of Bachelor of Science in Global Environmental Science.

THESIS ADVISOR

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Dr. Joshua Madin
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For my parents, Kate and Maksim, who were patient and understanding throughout this lengthy process. You both have provided me with examples of a strong work ethic and perseverance through adversity. For my wonderful close friends who not only understood the challenges but also the accomplishments of this thesis. For Devynn Wulstein and Dr. Joshua Madin, without your guidance and expertise this would have never been completed. For the Oceanography department, that instilled a deep desire within me to explore our planet and all its wonders. Finally, for all the future coral scientists. I hope my work will inspire you to protect our reefs in ways that I could not.

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ABSTRACT

Coral reefs and the ecosystem functions and services they provide are increasingly threatened by anthropogenic stressors. To counter these stressors, active reef restoration has become the emerging tool for reef scientists and managers to counteract coral loss at local scales. Currently, restoration focuses mostly on out planting corals in attempts to increase coverage and diversity to historical levels. However, there is only a basic understanding of the optimal sizes and densities of outplants that should be used for effective reef restoration. For instance, colony survivorship tends to be strongly associated with size. Thus, we believe that colonies grow fastest at low densities, where density-dependent processes like competition and disease are minimal. In this study, I use a meta-analysis and a field study to quantify the influence of coral density (or crowding) on colony survival. For the meta-analysis, I extracted data on the density and survivorship of corals from studies that measured both variables. For the field study, I used previously published data for 11 species from an eight-year demography study at Lizard Island on the Great Barrier Reef. For both data sets, I was able to quantify the relationship between density (individuals per meter) and survivorship (chance of surviving one year) by fitting linear models. For the field study, I was also able to include growth morphology (or growth form) as a covariate, which is traditionally thought to have a key effect on survivorship as density increases (i.e., some species are better competitors for space based on their shapes). However, I found that density had a negligible impact on coral survival in both sets of analyses, despite densities of up to 30 colonies per meter square and 100% crowding in the meta-analysis and field study, respectively. However, survivorship was indeed strongly related to growth form, where

robust massive forms tended to survive better than branching and tabular forms. These results suggest that competition for space is not a key driver of survival, and that other factors such as mechanical vulnerability override density processes. I ran into several issues with the meta-analysis that limited the amount of data I could analyze. For example, population density was reported in a range of different and incompatible ways, including as coral cover, which cannot reveal the difference between a single large colony and multiple smaller colonies. I therefore suggest that future efforts that measure coral cover should also include population density to improve data synthesis for meta-analysis. Overall, my work suggests that restoration initiatives should outplant colonies at sizes that optimize survivorship, which differ among species, and that outplant densities have little effect on survival rates.

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1.0 INTRODUCTION

1.1 Background

Coral reefs provide essential services to many human communities, including coastal protection, tourism, oxygen production, commercial and artisanal fisheries, and the aggregation of biodiversity. Reef ecosystems have become increasingly threatened by anthropogenic stressors on both the local and global scale (Rocha et al., 2018). Scleractinian corals are the engineers of these ecosystems but are estimated to be critically threatened by 2050 due to their vulnerability to climate change (Hoegh-Guldberg et al., 2017). Interventions (e.g., monitoring of inshore coral, water quality, aquatic plants, and pests, and guaranteeing updated coral information) and restoration efforts (e.g., installations of moorings and reef markers, predator control, increased in-field activity, geo-engineering actions, artificial structures, and reproductive recruitment activites) have been proposed in multiple regions, but the effectiveness of each method remains largely unknown (GBRMP Authority Progress Report 2018 and NAS Final Report 2019). Although limited in the scale they can be applied, reef restoration is one of the more promising interventions, but it also has yet to be fully optimized and implemented (Rinkevich 2008; Abelson 2006, and Rinkevich 2019). Many restoration efforts are based upon out planting fragmented “corals of opportunity” without explicit consideration of the niches open in the existing reef, or if the outplanted corals will survive in their new location (Boström Einarsson et al., 2020).

Although used interchangeably, restoration and rehabilitation have different meanings. Restoration is an attempt to restore an ecosystem (in this case a coral reef biome) that has been severely damaged, naturally or anthropogenically, back to its original state (Shaver et al., n.d.). Whereas rehabilitation is an attempt to repair damage, but not return it to its original state. The reason rehabilitation may be preferred over restoration can be due to lack of time and financial resources, as some restoration efforts rely on government funds which typically are only enough to cover short-term relief efforts (Hein et al., 2019). Prior to establishing mitigation protocals and techniques, reef managers need to identify the source of impact and put a conclusive end to the source in order to continue with a restoration effort. Any coral community that is environmentally impacted may not be considered for a restoration effort because the encological impacts will likely continue to harm the population (Precht & Robbart, n.d.) Thus, as climate change impacts coral reef ecosystems, rehabilitation efforts have to be increased and promoted. However, throughout the scientific marine community, the term ‘restoration’ is more popular to use with regards to coral reefs. Perhaps, that specific use of terminology defines the dire need and urgency for protection. Particularly, coral reefs possess cultural and economic value to coastal communities (Brander et al., 2007; “Coral Reefs,” 2003). Without the presence of these organisms, an estimated one billion people worldwide would be directly impacted (Cinner et al., 2018). Hence, the protection and full effort to restore the entire marine biome is an important issue as climate change rises and deteriorates marine ecosystems.

A reef restoration plan and design outline (Figure. 1) presented by the National Oceanic and Atmospheric Administration (NOAA) has a simplified 6-step plan on how to successfully outplant targeted coral species: 1. Set goal & geographic focus, 2. identify, prioritize & select sites, 3. identify, design & select interventions, 4. Develop restoration action plan, 5. implement restoration, 6. Monitor and evaluate progress (Shaver et al., n.d.). Current and proposed restoration efforts vary drastically (Ladd et al., 2016; Goergen et al., 2019; Goergen & Gilliam, 2018). A standard restoration protocol may pose as a difficult task due to the plethora of variables (i.e., pH, predators, community structure, genetics, sunlight, Sea Surface Temperature (SST), and nutrient availability) that can determine the success of coral survival (Baums, 2008; Forrester et al., 2013; Ladd et al., 2018; Rivas et al., 2021; Ladd, 2019). Commonly, a restoration project only focuses on one of the above variables and rarely on a combination (Calle-Triviño et al., 2021). This is because multiple variables affect each other and although observing one variable presents itself as a limitation in restoration efforts, it allows for restoration efforts to be completed in a timely fashion. To assume one variable is independent would be incorrect, because most metrics studied in coral ecology are dependent on one another. However, few studies evaluate the effect of population density on the vital rates of Scleractian corals (Edmunds et al., 2018). Interestingly, the current standards and interventions set out by NOAA lack a distinct consideration for coral population density and the potential effect it may have upon mortality.

To understand the effects of density-dependence on coral populations we must acknowledge what vital rates density can affect. Density depence is a biological process that influences population dynamics of an organism in a positive or negative way by affecting growth, mortality, fecundity or other rates. Not considering density-dependence as a significant variable in coral restoration efforts is a flaw because of its effect on important living metrics (Caley et al., 1996; Hixon et al., 2012). Currently, reef managers have gaps in knowledge as to what drives density dependence amongst coral reef populations (Ladd et al., 2018).

Although density-dependence is known to influence community dynamics, there are many methods to measure differences in density and populations. Understanding the metrics for growth, mortality, and recruitment is important yet, the current industry standard on how to gather and measure these data is flawed. For instance, most papers I observed in my meta-analysis (described below) focused on coral cover rather than density, and it was therefore difficult to draw conclusions about density-related processes. Understanding density dynamics is particularly useful in restoration efforts that are implemented after a significant disturbance event or when considering early life histories. Additionally, coral density provides a better understanding of how much coral truly exists (Birkeland et al., 2013). Without understanding coral population dynamics, it is difficult to assess why certain projects have success or failure. For corals, I refer to population density as the number of colonies in a particular area. Coral restoration is in its infancy and is yet mastered. Therefore, research needs to be continuously done to approach a baseline understanding for coral vitality in a variety of population states. With this approach, it will expedite restoration efforts and make them more effective. Ideally, reef managers would know the ideal population metrics for specific species and thus create suitable habitats and conditions for them.

To better guide out planting initiatives, the goal of my thesis was to explore the association between the density of corals and their vital rates, including survivorship, growth rate, partial mortality, and fecundity. I review these relationships in the following three sections (below). However, my thesis ended up only focusing on survivorship-density associations (survival and partial mortality), because the meta-analysis resulted in too little data for rigorous statistical tests of growth, partial mortality, and fecundity. Nonetheless, I analyzed data from a field study that captured survivorship as a function of density of neighbors of eleven species over six years to further support the meta-analysis I preformed. In each section below, I describe the considerations and influences that led to the pursuit of this review and analysis focus.

1.2 Impacts of Density on Coral Growth Rate

Varying population densities amongst coral reefs have been seen to impact the growth rate of Scleractinian corals in positive and negative ways (Shantz et al., 2011; Kopecky et al., 2021). For example, at lower population densities, the coral growth rate is traditionally hypothesized to increase due to a lower chance of competing with neighbors. Therefore, due to low population densities of coral, it is unlikely that the effects of competition between corals will be evident (Berryman et al., 2002). Competition for space and nutrients inherently causes the some coral species to die and may negatively impact the biodiversity of the reef (Chadwick & Morrow, 2011); e.g., monocultures may form. With less of a population density the threat of disease and competition decreases. However, a counter argument suggests that a reef with a larger density and small colony size (as seen through the process of fragmentation) shall increase the growth rate, specifically in staghorn coral species such as *Acropora cervicornis* (Lirman et al., 2014). Within this study, the literature reviewed measured the effect of density on coral skeletal growth by quantifying Total Linear Extension (TLE) – a process that documents the vertical growth of coral tissue and skeleton (Ladd et al., 2016). Growth rate is used as a metric to evaluate coral health. If growth is present during a restoration process, it is a valued indicator of a positive restoration technique. Yet, comparisons of different growth rates proved to be difficult because there is no single approach to measuring coral growth. Thus, any data collected needed to be converted into a common unit. This did not only apply to growth rates but to any vital measured.

1.3 Impacts of Density on Coral Survivorship

Natural and anthropogenic events often affect the survivorship of coral colonies (Adjeroud et al., 2018). Although survivorship is an excellent vital rate in a coral ecosystem, observing survivorship *in situ* is challenging. Determing a specific point of time in open water when a coral colony or fragment should be observed is difficult. At what point should survivorship be measured? With climate change increasing the presence of harmful natural events, it may become laberous to determine when the colony survived if the act from which they survived is not tangiable (such as increased SSTs). Evidence confirms that rising SSTs have put stony corals into significant stress which increased their vulnerability and makes them susceptible to coral diseases (Selig et al., 2010; Ward, Kim, and Harvell 2007; Haapkyla et al. 2011; Burge et al. 2013; Burge et al. 2014). Disease ridden corals are seen with decaying coral tissue or a colored band - black, yellow, white, or brown (Sziklay, 2017). With limited research on coral immunity, it is not fully known whether coral species can recover post infection, although some have shown signs of recovery (Ruiz-Diaz et al., 2016; *Reef in Recovery Window after Decade of Disturbances | AIMS*, n.d.). What is known is the fact that climate change and rising oceanic temperatures promote the prevalence of such diseases in coral communities. If there is a significant rate of disease in high dense coral populations, it will likely lead to low survivorship rates within the affected community.

Previously mentioned, competition amongst coral affects their growth rate. Coral competition is usually over available resources and can occur between other species of coral, algae, sponges, and ascidians (Chadwick & Morrow, 2011). This interaction can affect a community by changing demographics and dynamics of the reef ecosystem (Horwitz et al., 2017; Chadwick & Morrow, 2011;Álvarez-Noriega et al., 2018). However, studies have demonstrated that competition within a coral reef community has little effect on the coral vital rates due to the complexity and temporal extent of this interaction (Precoda et al., 2017; Horwitz et al., 2017; Chornesky, 1989).

Apart from competition and disease, life history also has the potential to influence survivorship. A study revealed that juvenile corals and fragmented corals have higher survorship rates in smaller densities (Idjadi et al., 2010). Perhaps, this finding is explained by the fact that smaller size classes of coral require less resources than larger colonies and therefore, they will experience less opportunity of competition.

1.4 Impact on Density on Coral Fecundity

Fecundity is a critical demographic trait in coral communities. The presence or absence of fecundity determines the fitness of the coral community. In theory, density and fecundity should have a direct relationship. Studies reveal that as the density level increases within a coral community, the fecundity of the coral is expected to as well (Álvarez-Noriega et al., 2016; Birkeland et al., 2013). On a global scale, corals in the Caribbean have seen reduced rates in fecundity as the population decreases. These findings are from as early as 1977 to 2004 (Hughes & Tanner, 2000; Bak et al., 2005; Gardner Toby A. et al., 2003). It should be noted that, although the results imply that high densities promote high fecundity, it is entirely dependent on environmental and external factors. Infact, research on *A. millepora* showcases that fecudity does not improve regardless of density levels (Doropoulos et al., n.d.). However, other species of coral may have opposite reactions to varying population density levels. For reef managers, it is critical to manage reef densities and populations if fecundity is dependent on it, because it will encourage coral populations to grow. Perhaps, certain species of coral will benefit from lower densities, because a decrease in coral cover will increase larval recruits due to the availability of space. Coral fecundity might also increase in higher coral populations. Regardless, it is necessary to observe and take note of patterns. A significant cause for concern will occur once the coral population diminishes and fecundity will cease.

2.0 METHODS

The methods are separated into two sections. First, I describe the scaled meta-analysis and detailed process of including literature for this analysis. Studies included in the meta-analysis were done in Miami, Florida Keys, U.S Virgin Islands, Puerto Rico, Jamaica, Curaçao and British Virgin Islands. All these regions are encompassed by the blue circle. However, only the data from the Miami and Florida Keys Region was included in an analysis as designated by the red circle (Figure 2). Second, I detail the multi-year data collected from Lizard Island (Figure 3) on the Great Barrier Reef and the methods used to analyze the survivorship relationship. These two datasets are not comparable because the metrics for measuring population density or competitive effects are not compatible.

2.1 Meta-Analysis

This pilot systematic review and meta-analysis was informed by the procedure formulated by Tuttle et al., (2020) which included the Guidelines and Standards for Evidence Synthesis in Environmental Management, version 5.0 and the procedures of Reporting standards for Systematic Evidence Synthesis (Haddaway et al., 2018).

2.1.1 P.E.C.O

In order to properly complete a global systematic review and a meta-analysis, we aimed to follow the protocol defined in Tuttle et. al., (2020) and utilized in Nalley et. al., (2021).Yet, our method of collecting literature had to be adjusted because a substantial number (>10,000) of results were appearing for only a single search term. To simplify the searches and perform a scaled-down approach, we applied our search terms to Google Scholar. Our search terms, the resulting literature, and our filtration process are defined in the sections below. Here, we establish our main focus and investigation questions: (1) What are the coral density-dependent health relationships; and (2) How does density affect different responses amongst the global coral populations. Our PECO and Guiding questions followed a similar established protocol (Tuttle et al., 2020). In this study we are investigating the following:

1. What are the responses associated with change in coral population density?

1. Do these responses differ by taxa or coral morphology?
2. Do the responses differ by life histories?
3. Do the responses differ over time?
4. Do the responses differ by geographical location?

Population:

We are studying Scleractinian corals, photic, meso-photic corals. No soft corals will be taken into consideration.

Exposure:

We will observe higher density or change in density that is positive in coral communities through observational and manipulative data.

Comparison:

To conduct a proper comparison, reef patches with different densities or health will be contrasted in order to determine low density.

Outcomes:

At all possible endpoints, physical, physiological, behavioral, ecological, and species richness response due to density is documented thoroughly to determine the impact on coral vital rates.

Limitations:

Our scaled approach does not enable us to make global comparisons or make statements relating the ubiquity of coral responses to density, as this study only relied on one search engine and 59 results. Additionally, the non-existence of data or the presence of literature written in another language besides English without a proper translation will limit the research.

2.1.2 Defining Search Terms

30 search terms were created using a Boolean system. Each search term consists of the word "CORAL" in order to generalize and consider all genera and species of coral. By conjoining each search term with "AND", we were able to narrow our results in order to obtain narrowed results. Our search terms were specifically chosen to focus on the vital rates of Scleractinian corals and how coral populations are naturally affected by change in population density

2.1.3 Data Extraction for Meta-Analysis

The search terms (Table 1) were applied to Google Scholar where 59 relevant results were recorded. As an initial filtering stage, each paper abstract was analyzed for potential relevance via the categories defined in Table 2. Abstract relevance was determined based upon the PECO described above and particular coral responses were recorded. Nine articles were chosen as adequately meeting the standards described above for investigating the effects of density on the vital rates of Scleractinian corals.

In this analysis, I define the term 'responses' to be considered anything that low, moderate, or high population density may affect such as: growth, mortality, fecundity, survivorship, recruitment. Coral responses were grouped together by similarity and comparability. Due to the limitation of only using one search engine, my search results were quite small and thus, an unintentional data bias was formed. As, ultimately there was only a single species of coral studied within the accepted literature. To resolve and avoid the bias, we analyzed morphology specific survival data from the Great Barrier Reef . Although the results of this pilot study cannot provide generalizable results it can be used to direct research and inform more intensive systematic reviews.

2.2 Data Extraction

Coral responses to the density metrics reported were extracted from the nine papers we accepted for the meta-analysis. The extraction and data organization process followed the procedures detailed in Nalley et. al., (2021), see supplemental material therein. Data was extracted via an internet-based data extraction tool (WebPlotDigitzer version 4.3). In order to standardize the effect of density-dependence upon coral vital rates we excluded density metrics that were inadequate or not comparable to the absolute measurement of population density (# coral colonies / meter^2). The incomparable metric included coral cover and studies that did not fully define their area of study. Responses were also grouped by comparability and conversion. Although we extracted responses related to recruitment, coral disease, and growth rates, we were unable to create meta-analyses of these results due to the lack of comparison between studies in terms of the response or the stressor (i.e., density). Only survival (percent of colonies within study) and partial mortality (percent tissue mortality within study) had comparable enough metrics to enable a meta-analysis (Table 7 & 8) .

2.2.1 Coral Response Selection

For each identified response variable we extracted the following information to assess the potential for comparative analysis: response variable unit of measurement, study duration, population density, population density unit of measurement, and potential for conversion. Table 7 shows the relevant studies related to the survival response. The time-point of the studies differed, some using yearly and others monthly (reported in decimals), therefore we converted the survival response to account for the differences in time. Density values shown are converted values rather than raw extraction from the studies. Partial mortality values and metrics are recorded in Table 8. The remaining extracted response variables are grouped together under a miscellaneous section (Table 9). Due to the lack of accepted studies, based upon the above criteria, we are unable to perform comparative and aggregated analyses on these responses.

2.3 Lizard Island Demography Study

Coral survivorship data were collected over a five-year period from 2008 to 2013 on the semi-exposed reef crest of Lizard Island in the north of the Great Barrier Reef (GBR; 14.699839° S, 145.448674° E) following the methods and procedures detailed within (Álvarez-Noriega et al. 2018; Madin et al. 2014; Álvarez-Noriega et al. 2016; and Dornelas et al. 2017). The colony level data is grouped by five morphologies: massive, digitate, corymbose, branching, and tabular. Competition was estimated as the proportion of a colony's perimeter interacting with other corals, which ranges from 0 (no contact with neighbors) to 1 (whole perimeter contacts a neighboring coral). Survival was binomial, coded as 0 if the coral died in the following year or 1 if it survived the following year.

2.4 Analysis of Results

All statistical analyses and graphical data representations were done in R (R Core Team, 2022). The survivorship data for the meta-analysis was already in terms of percent survival, but was converted to the same time scale by raising survivorship to the power of (1/time in units of months), which allowed us to fit the density relationship with a binomial regression using the glm function in R. We initially included the study as a factor, but Akaike Information Criterion (AIC) values revealed no benefit to including the term. Additionally, we performed an analysis of variance on the model output via the anova function in R (Table 6).

Similar to the survival analysis we fit the partial mortality as a function of density with a linear regression (glm function) including the study as an interaction (Figure 5). There was a study that had an unreasonably large density value and we decided to consider that as an outlier and not include it in the regression fit.

The data from the multi-year study done on survival and competition data were fit to a logistic regression via the glm function with family equals binomial. Crowding (a proxy used for density levels), growth form (morphology), log(area), and the quadratic term of log(area) were included as interaction terms in the model following the methods defined in Madin et al., (2014) (Table 6). Statistical significance was analyzed through an analysis of variance (ANOVA) (Table 5) .

3.0 RESULTS

3.1 Meta-analysis Results

3.1.1 Survival

Figure 5 represents the relationship between survival (% colonies) of *Acropora cervicornis* coral in relation to density (colonies/m^2). Although there is a slight positive slope (Figure 4) the relationship is not significant. As supported by the ANOVA results (Table 4), all p-values are > 0.05.

3.1.2 Partial Mortality

There is a noticeable relationship between population density (colonies/m^2) and partial mortality (% tissue) (Figure 5). The positive slope indicates that as density increases, the percent of partial tissue mortality increases. Additionally, we noticed a similar lack of significance between density and partial mortality. However, there is a significant relationship when the study is included as a factor ($p < 0.05$) (Table 3).

3.2 Lizard Island Results

We hypothesized that crowding would be a major component to the survivorship of the corals within this study and that there would be a difference between the response of the growth forms. However, we see no significant effect on survival due to crowding (Fig 6A and Table 5&6), therefore refuting our initial hypothesis. Similar to the results published in earlier studies of this reef, growth form and planar area are significant factors in determining the survival response (Fig 6B and Table 5&6) (Álvarez-Noriega et al. 2018; Madin et al. 2014; Álvarez-Noriega et al. 2016; Dornelas et al. 2017).

4.0 DISCUSSION

Both the meta-analysis and the field study showed that survivorship of corals was independent of density. The result is striking, because there is a long history of research about the role of density-dependent processes in structuring reef coral assemblages (refs). For restoration and out planting, these analyses suggest that the size of coral outplants is far more important for survivorship than the density at which they are outplants, where an optimal size will differ among growth forms. Therefore, outplant density can instead be determined by other factors important for restoration, such as outplant capacity (e.g., how many outplants there are for how much area of reef).

The results refute our original hypothesis that survivorship be density dependent. Nonetheless, it is in agreement with recent results detailing the negligible relationship between competition and colony growth (Álvarez-Noriega et al., 2018). Although the results corroborate this previous study based on survivorship, they remain surprising because we did expect for crowding to influence survivorship. Instead, we saw that the trait-based variables such as colony growth form impacted survivorship more strongly.

A 2014 study evaluates the influence life histories and structural variation has on the survivorship of coral colonies (Madin et al.). From that study, mortality rates not only vary based on structural differences but size classes as well. We noticed that tabular coral colonies had a declining curve with respect to their survival probability as their colonary planar area m^2 (log10) increased (Figure 6B) which we can assume relates to their mechanical vulnerability. From the generated graph (Figure 6B), it is believed that tabular coral colonies are more susceptible to higher mortality ratesdue to their top-heavy structure as adults. Massive coral colonies are more stable since their weight is targeted towards the bottom and they can withstand physical impact (Madin et al., 2014). Strictly focusing on growth form (Table 6), we notice that our results suggest that Massive and Tabular coral structures do indeed have an effect on the survivorship of the colony. Moreover, in the graph (Figure 6B) we noticed that the lines corresponding to each morphology appear to be ranked according to the fitness of their own mechanical vulnerability. Our meta-analysis only focused on studies of *Acropora cervicornis*, due to the large body of work performed on this species, which has a branching morphology and can be considered in terms of mechanical vulnerability as well. The tops of the coral head break off easily, thus causing a decrease of colony survival, or an increase in partial mortality. Yet, colonies still survive because branching corals utilize, fragmentation as a form of asexual reproduction (Omer et al., 2020). Additionally, mechanical vulnerability would not impact the survivorship of coral colonies if the size-class corals were smaller such as juveniles as opposed to adults (Million et al., 2021; Kopecky et al., 2021). Despite the morphology of a specific coral, if the coral size is small it could withstand physical impact, because the mass of the coral would theoreticlally be centralized and not widely dispersed as it with adult corals. Perhaps, if the concentration of coral colonies was composed of juveniles at a high density the results would reflect a strong positive linear slope demonstrating a direct relationship between density-dependence and survival. Further observations and testing would need to be conducted to either confirm or deny this hypothesis.

Mechanical vulnerability seems to be a notable parameter when establishing a density-dependent relationship. Although none of the metrics within the small scale study included differences in morphotypes. Each study involved the species *A. cervicornis,* and therefore we can draw conclusions from the multi-year study and argue that the lack of a density-dependent relationship on the survival of Scleractinian coral is influenced by the branching structure (similar to tabular and massive growth forms)

4.1 Limitation and Gaps

Our study suggests that although density-dependence does not influence coral growth, survival, or partial mortality as an independent variable it does impact reef building communities. Although, because of the structure of this review, there are a notable amount of limitations that affect the universality of these results. Firstly, we are limited by the lack of comparable studies. If following the more rigorous systematic review format, we would have found a broader range of usable results and we suggest that future steps be taken to do so as to support our results or find clearer instances where they are refuted. Furthermore, there is no standard on the recording of population density data. We noticed that coral population density is a neglected parameter and coral cover is the popular metric chosen to quantify the coral colonies present. By using coral cover as a measure of density, it leads to a bias because coral cover is not a dependable parameter since a distinction between a single large coral colony and many smaller coral colonies cannot be made. In fact, the multiple variations in how density was cataloged led to data that could not be converted nor compared. This then limited the usable data available in the small-scale analysis. Additionally, within the small scale meta-analysis, the primary species studies was *Acropora cervicornis,* a well studied branching coral, in the southern Atlantic regions (Goergen & Gilliam, 2018; Goergen et al., 2019; Ladd et al., 2016; Ladd et al., 2019; Huntington et al., 2017; Drury et al., 2019; Edwards et al., 2015; Unsworth, 2020; Vardi, 2011) but the data set from the GBR encompassed many Scleractinian coral species, but focused on different morphologies rather than species-specific effects. Majority of the literature cited involves *Acropora cevicornis* because of its characteristic traits such as asexual reproduction and fast growth rate (Goergen et al., 2020) and its importance to restoration efforts in the Atlantic. A broader range of species-specific data would enable a more universal comparison of the impacts of density on coral vital rates.

5.0 CONCLUSIONS

As climate change intensifies the remaining global coral populations are expected to decline due to alterations to the marine ecosystem. Natural reefs (ones not defined by coral restoration efforts) may rarely reach density levels where competition or crowding could have a significant effect (30 - 50 % coral cover typically defines healthy reefs). Yet, restoration efforts may pose a future coral reef with much higher coral cover. Thus, it is important to understand coral characteristics and demographic traits to better facilitate and improve restoration efforts. Although our results show no clear relationship between adult colony survival and population density, we argue that there are potential factors not considered in regard to the relationship between coral demographics and density. With regards to restoration practices, reef managers may fail to consider ideal density levels for coral out plantation which can serve to limit coral husbandry.

Although not studied within this thesis, coral juveniles may be more impacted by density than adult corals. We encourage restoration managers within the coral ecological field to regard this study as a guide and foundation to establish research with a considerably larger data set to achieve the goal of a better understanding on how and if density truly affects the vital rates of Scleractinian corals. Most importantly, future coral collection efforts need to evaluate how to report population density. We encourage coral reef scientists to incorporate a measure of population density in addition to coral cover to establish a more standard process that will allow a comprehensible analysis of density-dependent relationships.

Appendix

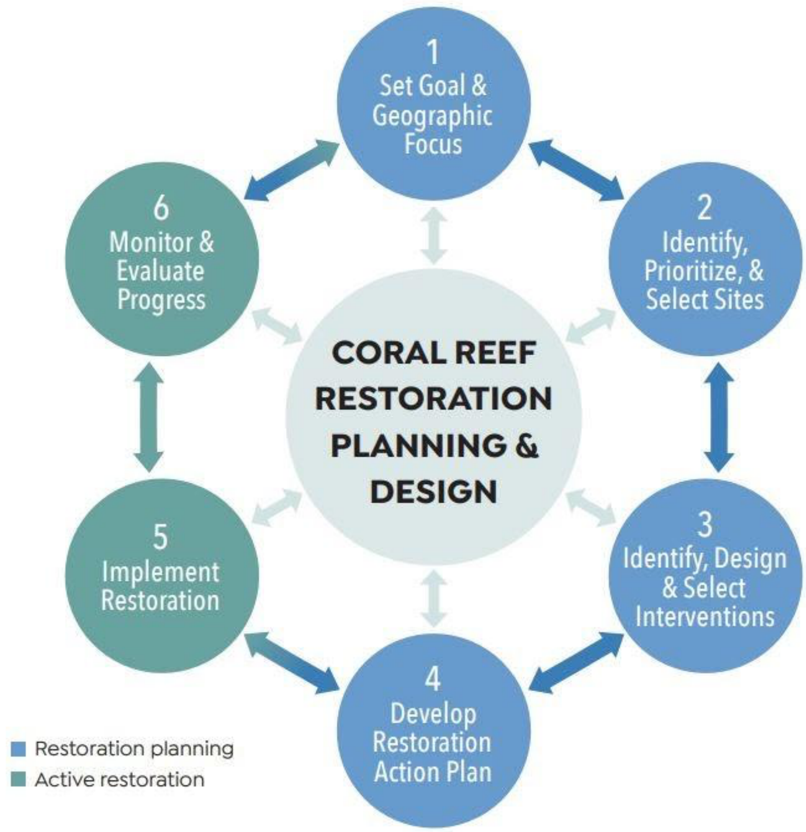

Figure 1. A method of coral reef restoration proposed by NOAA. The 6-step plan is divided into two sections: 1) restoration planning 2) active restoration. Steps 1 - 4, refer to restoration planning and steps 5-6 refer to active restoration (A Manager's Guide to Coral Reef Restoration Planning and Design, n.d.)

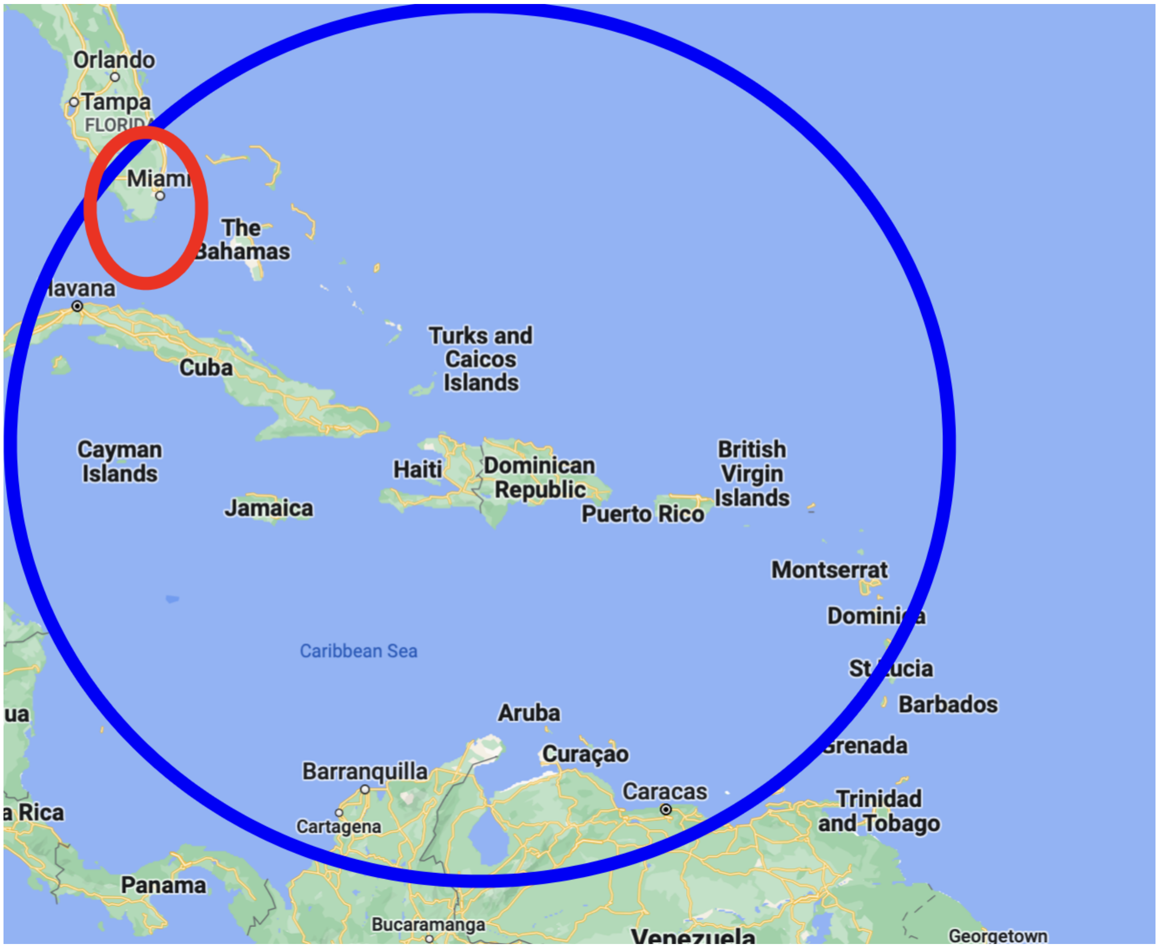

Figure 2. A geographical representation of the area where Acropora cervicornis is located based on the literature gathered for this specific meta-analysis. The large blue circle encompasses all the locations from the literature found. The smaller red circle correlates to just the Miami and Florida Keys region. This is with respect to the literature from which the data was taken and used to make analyses.

Figure 3. The location of Trimodal Reef (14.6993 ºS, 145.448674 ºE) off the southern coast of Lizard Island, Australia in the Great Barrier Reef Region. Data was collected by Mariana Álvarez-Noriega (2008) and Dr. Joshua Madin (2009).

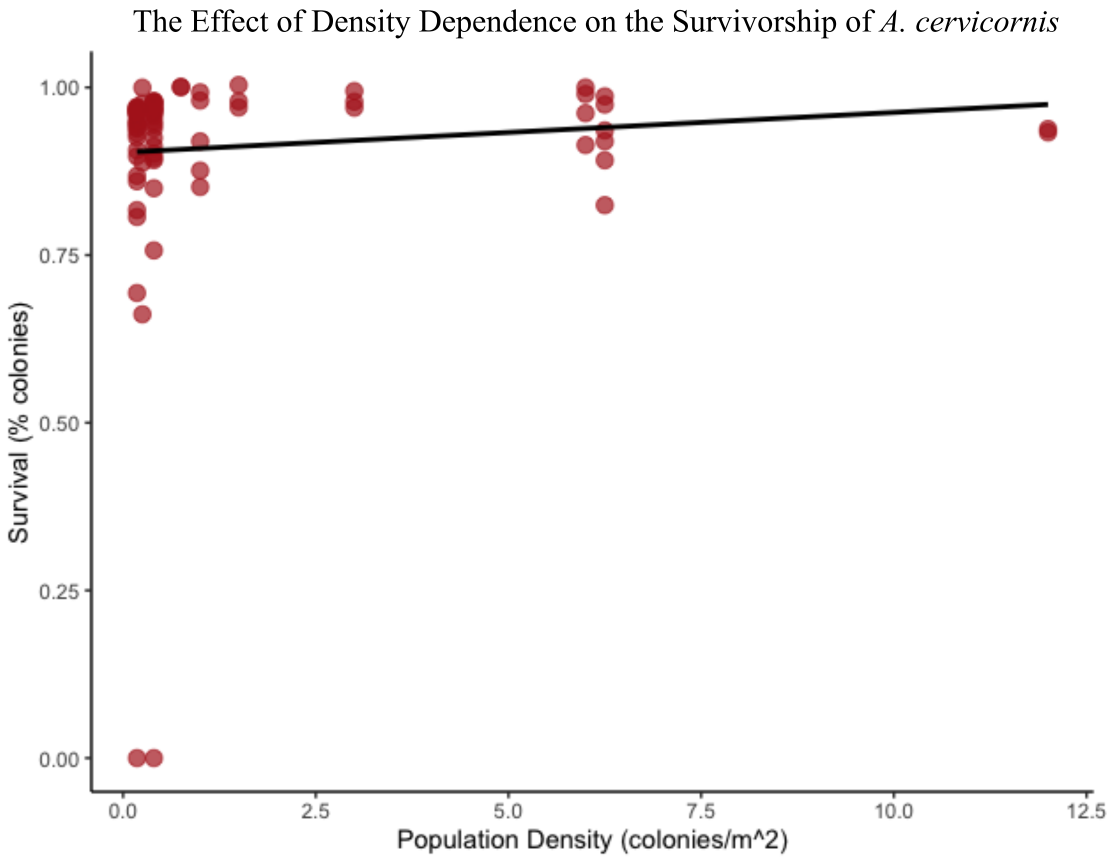

Figure 4. A simplified linear modeling showing the relationship between population density (colonies/m^2) and survival (% colonies). The line of best fit appears to have a slight positive slope. Two clusters are seen at the lowest population density and the average amount of colonies/m^2.

The Effect of Density Dependence on the Mortality of *A. cervicornis*

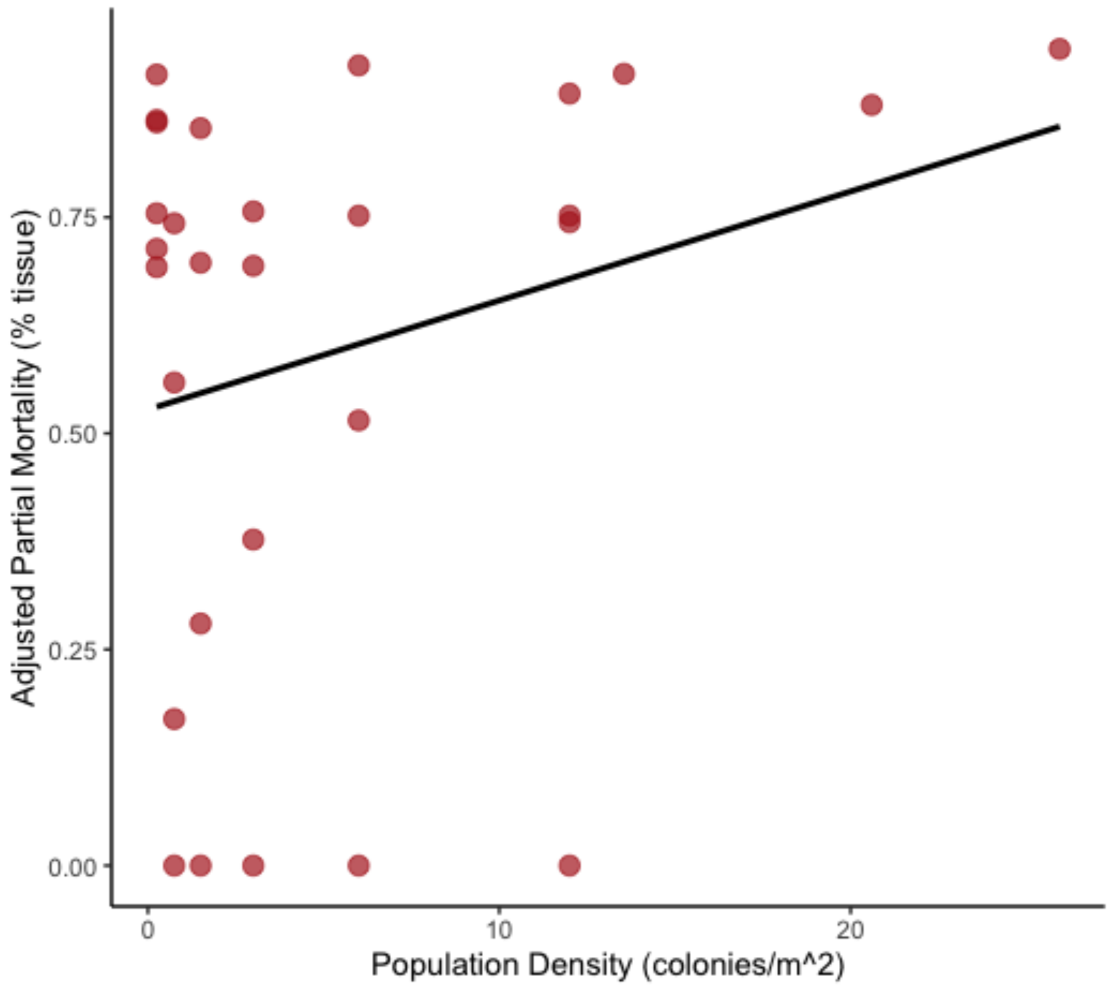

Figure 5. A scatter plot depicting the effects of density on the mortality of Acropora cervicornis corals. The x- axis relates to population density (colonies/m^2) and the y – axis relates to the adjusted partial mortality (% tissue). Data was adjusted to remove an outlier due to a different collection method from a specific study (Ladd et al., 2016; Huntington et al., 2017; Goergen and Gilliam, 2018).

Figure 6: A statistical analysis of the Trimodal results demonstrating that crowding has a negligible effect on survival. Figure 6A demonstrates the relationship between crowding and survival probability. Based on the graph, there is hardly any change in survivorship. However, graph 6B demonstrates that as the colony planar area increases so does the survival probability in a rather exponential way.

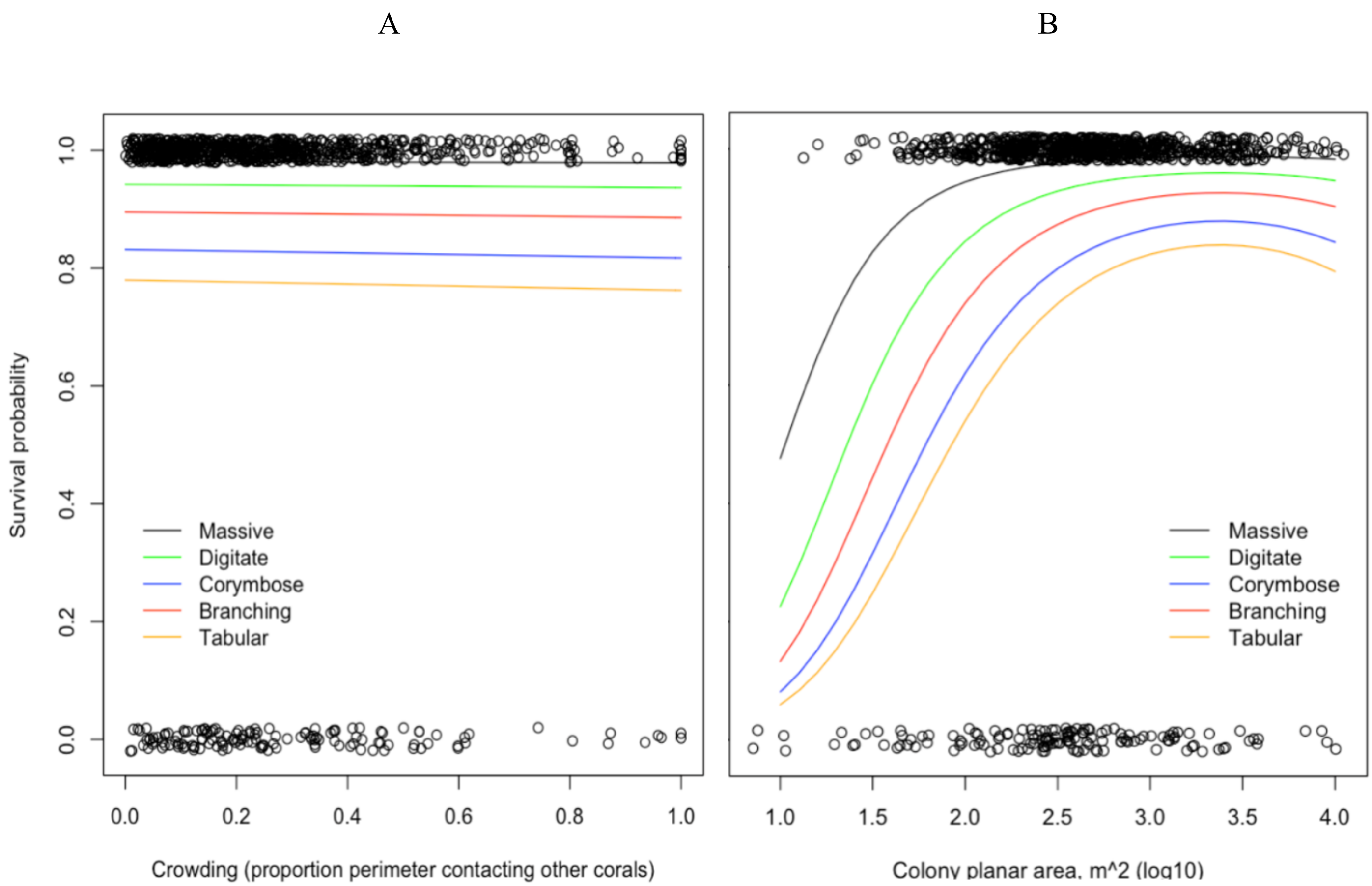

Table 1. Search Terms.*The list of search terms implemented in this study. The Asterix(*) next to certain search terms is used as a placement holder for different endings. These search terms were a list that resulted in only 59 results within google scholar but > 10,000 in other databases that included results from "gray" literature.*

coral	AND	population	AND	density
coral	AND	cover		
coral	AND	density - dependence		
coral	AND	density - dependence	AND	mortality
coral	AND	density - dependence	AND	growth
coral	AND	restorat*		
coral	AND	density - dependence	AND	fusion
coral	AND	outplant*		
coral	AND	diversity		
coral	AND	survey		
coral	AND	density - dependence	AND	species-richness
coral	AND	population	AND	cover

Table 2. Paper Extraction Responses. *Example categories for the literature filtration phase. We characterized the studies by evidence of population density measurements, coral responses and other potentially important factors. This was the second stage in our literature acceptance process.*

Study Type	# Of Coral Taxa	Genera	Is density Measured?	Community Study?	Coral Response 1	Coral Response 2	Coral Response 3	Coral Response 4

Table 3. Partial Mortality ANOVA TEST *An ANOVA test for the best fit model. We tested parameters (Partial Mortality with respect to Density and Partial Mortality with respect to different literature sources that highlighted Partial Mortality in their studies) to determine which is statistically significant on survival. Our p-value was set to (0.05) to make deductions. Only one of these parameters is statistically significant.*

	Df	**Dev. Resid.**	**Df Resid**	**Dev.**	**Pr(>chi)**
NULL			28	3.1096	
PartialMort_Density	1	0.19487	27	2.9148	0.13875
PartialMort_RefID	2	0.69195	25	2.2228	**0.02042**

Table 4. Survival ANOVA TEST *An ANOVA test for the best fit model. We tested parameters (Survival with respect to Density and sSurvival with respect to different literature sources that highlighted survival in their studies) to determine which is statistically significant on survival. Our p-value was set to (0.05) to make deductions. Only one of these parameters is statistically significant.*

	Df	**Dev. Resid.**	**Df Resid**	**Dev.**	**Pr(>chi)**
NULL			80	2.0308	
Meta_Survival_Density	1	0.018794	79	2.012	0.3905
Meta_Survival_RefID	2	0.049702	77	1.9623	0.3771

Table 5. GBR ANOVA TEST *An ANOVA test for the best fit model. We tested parameters (crowding, growth form, and area) to determine which is statistically significant on survival. Our p-value was set to (0.05) to make deductions. Only 2 out of the total 3 parameters are statically significant.*

Parameter	Df	Dev. Resid.	Df Resid.	Dev.	Pr(>chi)
NULL			904	783.08	
crowding	1	1.51	903	781.57	0.2192
growth_form	4	24.7	899	756.87	**<0.0001**
poly(area_log10, 2)	2	48.723	897	708.15	**<0.0001**

Table 6. Logistic Regression Summary Table *A statistics summary displaying the independent tested variables as rows and the data variables as columns. Independent variables included colony area and different coral morphologies. Statistics were run in RStudio.*

Coefficients:	Estimate	Std. Error	Z Value	Pr (> |z|)
(Intercept)	1.93375	0.32897	5.878	**< 0.0001**
crowding	-0.09812	0.45167	-0.217	0.8280
growth_form_Corymbose	-0.54939	0.33022	-1.664	0.0962
growth_form_Digitate	0.64267	0.39543	1.625	0.1041
growth_form_Massive	1.78187	0.55041	3.237	**0.0012**
growth_form_Table	-0.88177	0.35547	-2.481	**0.0131**
poly(area_log10,2)1	17.90449	3.42043	5.235	**<0.0001**
poly(area_log10,2)2	-9.53095	2.91528	-3.269	**0.0011**

Table 7. Survival. *Responses found from the literature review. This metric was measured as a percent of all the surviving corals out of the entire colony. Each study measured density differently. To make it comparable, density levels were converted. The RefID correlates to the citation. It was used as a marker to distinguish valued material for the small-scale meta-analysis. *2 high density patches greater than <1 hectare each*

Response Variable	Units of Measurement	Duration (months)	Density	Units of Measurement	Convertible?	Citation/ RefID
Survival	Percentage	0,3,3,7	.75 1.5 3 6 2	Corals per m^-2	yes	Ladd et al. 2016/ DD01
Survival	Percentage	12,24	0.25	Corals per m^2	yes	Goergen and Gilliam, 2018/ DD33
Survival	Percentage	98	0.18 0.4	Corals per m^2 *	yes	Goergen et al., 2019/ DD13

Table 8. Partial Mortality. *Responses gathered from the cited literature that focused on partial mortality. Density was convertible and comparable. The RefID correlates to the citation. It was used as a marker to distinguish valued material for the small-scale meta-analysis*

Response Variable	Units of Measurement	Duration (months)	Density	Units of Measurement	Convertible?	Citation/ RefID
Partial Mortality	(% of Colony w/o live tissue)	0,3,7,13	.75 1.5 3 6 12	Corals per m^-2	yes	Ladd et al., 2016 / DD01
Partial Mortality	(% of Colony w/o live tissue)	24	84.45 13.55 25 95 20.6	Corals per m^2	yes	Huntington et al., 2017/ DD04
Partial Mortality	(% of Colony w/o live tissue)	12,24	0.25	Corals per m^2	yes	Goergen and Gilliam, 2018 / DD33

Table 9. Miscellaneous. *Responses that were not applicable to the meta-analysis because they were unique to each individual literature source and could not be compared.*
**2 high density patches greater than <1 hectare each*

Response Variable	**Units Of Measurement**	**Duration (months)**	**Density**	**Units of Measurement**	**Convertible?**	**Citation/ RefID**
Juvenile Corals	50 m^-2	1	Juvenile Corals	50 m^2	yes	Ladd et al., 2019/ DD03
Shannon Diversity Index	Percent cover	11 12 13 14	Percent cover	1 m grids w/ masonry lines	no	Drury et al., 2019/ DD08
Bleaching	Percentage	1, 8, 12	Percent cover	2 m grids w/ masonry lines	no	Drury et al., 2019/ DD08
Settlement	No. per 0.1 m^2	0.083, 0.416, 2.5, 3	Absolute corals	0.1 m^2	yes	Edwards et al., 2015/ DD10
Settlement vs. Recruitment	No. per 0.1 m^2	0.083, 0.416, 2.5	Absolute corals	0.1 m^2	yes	Edwards et al., 2015/DD10
Larval Density	No. per 0.1 m^2	0.416, 2.5	Absolute corals	0.1 m^2	yes	Edwards et al., 2015/DD10
Recruit Density	m^-2	7, 5	Absolute corals	0.1 m^2	yes	Edwards et al., 2015/DD10
Disease Prevalence	Percentage	12, 24	absolute colonies	4 m^2	yes	Goergen & Gilliam, 2018/ DD13
Predation Prevalence	Percentage	12, 244	absolute colonies	4 m^2	yes	Goergen & Gilliam, 2018/DD13

Volume Expansion	Ellipsoid Volume	7	Absolute coral fragments	cm	no	Unsworth, 2020/ DD20
Fragment Productivity	Ellipsoid Volume	4	Absolute coral fragments	cm	no	Unsworth, 2020/DD20
Relative Abundance	Size class	84 36 36 72 36 12	Absolute individual corals	cm	yes	Vardi, 2011/DD26

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