Predicting shifts in demography of *Orbicella franksi* following simulated disturbance and restoration

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Abstract

Disturbances of coral reefs are increasing in frequency, intensity, and duration. These changes will likely result in demographic shifts in many populations of reef-building corals with unknown consequences for ongoing coral restoration efforts. To address this knowledge gap, here we use empirically derived stage-based matrix population models to predict how a relatively stable population and areal coverage of *Orbicella franksi* may change under simulated disturbance and restoration scenarios. Overall, simulated restoration outplanting greatly increased the number of *O. franksi* colonies and overall estimated areal coverage when compared to baseline population estimates. Under a mild disturbance scenario, the number of *O. franksi* colonies were projected to decrease by up to 90% by 2050, but simulated restoration was predicted to offset the loss in number of colonies. Under a severe disturbance scenario, the number of *O. franksi* colonies also decreased, but simulated restoration efforts were not able to offset colony losses. Under both disturbance scenarios there was a large projected loss of *O.*

franksi areal coverage even when restoration was implemented. However, restoration prevented a rapid decrease in number of colonies in the severe disturbance scenario. These findings highlight the potentially catastrophic effects of disturbances on previously stable coral populations, and the role restoration can play in mitigating these threats. Increasing studies focused on widespread ecological and demographic monitoring of disturbed and restored corals will be critical in the development of more effective restoration strategies for conserving these threatened species in an uncertain future.

Key words: coral reefs, demography, disturbance, matrix population models, *Orbicella franksi*, restoration

1. Introduction:

Climate change is altering the dynamics of marine populations. In marine systems, climate change is altering abiotic disturbances (e.g. storm intensity) and exacerbating stressors (e.g. increasing temperatures and decreasing dissolved oxygen), creating challenges for the long-term persistence of marine species and ecosystems (Keister et al. 2000, Schmidtko et al. 2017, Raven et al. 2020). In many instances, the rate of change of environmental conditions can occur faster than species can adapt, leading to a loss of biodiversity and ultimately loss of ecosystem functions and services (Hooper et al. 2005, Harley 2011, Cook et al. 2014). Benthic species unable to shift their spatial distribution at rates similar to shifts occurring in the environment are at higher risk of population decline as compared to relatively mobile species (Levin 2006, Atkins and Travis 2010, Harley 2011, Lewis et al. 2021a). While many sessile marine species have a larval dispersal stage as part of their life history, such larval stages are relatively passive compared to advective forces and largely reliant on ocean currents to transport them to more favorable habitat. After the larvae of some of these species settle, they grow to create complex biogenic habitat, serving as foundation species that support a diversity of organisms (Ellison et al. 2005, Slattery et al. 2011, van Katwijk et al. 2016).

Foundation species play a critical role in structuring and supporting complex marine ecosystems and their loss can result in severe negative effects on higher trophic levels (Ellison et al. 2005, Duke et al. 2007, van Katwijk et al. 2016). Stony corals, the foundation species of coral reef ecosystems, are highly imperiled by climate change (Bindoff et al. 2019, Maher et al. 2020). These species vary in geographic range and life history strategies, but in terms of survivorship, many can only survive within a relatively narrow range of water temperature and light availability; a degree or two increase in temperature can lead to massive coral bleaching events

(Glynn 1993, Baird et al. 2018, Hughes et al. 2018c). Extreme coral bleaching events used to occur relatively infrequently, but now are predicted to occur every six years globally (Hughes et al. 2018b). Due to these myriad threats, tropical coral cover loss is estimated at 50-75% globally (De'Ath et al. 2012, Hughes et al. 2018b, Bruno et al. 2019).

Additional threats to corals include hypoxic events, disease outbreaks, algal overgrowth, severe storms, and predation, all of which may pressure a population simultaneously (Bruno et al. 2007, De'Ath et al. 2012, Glynn et al. 2020). Further, the increase in prevalence of diseases, namely stony coral tissue loss disease (SCTLD) has led to extreme colony loss of highly susceptible corals and is spreading rapidly in many regions (Muller et al. 2020, Brandt et al. 2021). These compounding and interacting factors make determining the true driver of coral loss and mortality complicated. Together, disturbances (e.g., extreme storms and hypoxic events) have resulted in coral cover losses ranging from 5% to 60% (Hughes et al. 2018c, 2018b, 2018a, Johnston et al. 2019b). While coral reef systems have evolved mechanisms to recover from natural disturbances, the frequency and magnitude of disturbances in recent years suggests active restoration and conservation efforts will be increasingly important to help sustain and ensure these foundation species continue to exist in nature (Glynn 1993, Slattery et al. 2011, Bostrom-Einarsson et al. 2018).

To combat coral loss the practice of restoration is increasing (Bostrom-Einarsson et al. 2018). Direct interventions, including restoration, along with natural and assisted adaptation are now considered necessary for corals and coral reefs to survive the climate crisis (NASEM 2019). To date, coral reef restoration has been dominated by coral gardening, which involves transplanting coral fragments, primarily branching corals, following a nursery phase (Bostrom-Einarsson et al. 2018). In recent years, additional restoration techniques have emerged and efforts to restore massive non-branching corals, such as *Orbicella franksi*, have increased. Augmenting coral species richness on a degraded reef can have multiple synergistic benefits, and enhance the resistance and resilience of a reef to bleaching and fragmentation (Clements and Hay 2021). Furthermore, massive corals increase the physical stability of the reef structure (Bostrom-Einarsson et al. 2018) and can contribute substantially to reef accretion. However, it remains unclear how restoration of massive corals impacts population growth rates, and how effective restoration may be at mitigating colony losses caused by disturbances.

To address this knowledge gap, size-structured matrix population models were developed for *O. franksi* using empirical data describing vital rates (i.e. survivorship, mortality, growth, etc.) in the northwest Gulf of Mexico (Caswell 2001, Vardi et al. 2012, Riegl et al. 2017, Edmunds 2019). More specifically data collected within the boundaries of the Flower Garden Banks (FGB) were used to forecast demographic shifts in *O. franksi* population structure under different scenarios simulating future disturbance regimes and restoration scenarios. Due to the relative paucity of coral vital rate data, demographic models have been underutilized in coral reef ecology (Edmunds 2019, Edmunds and Riegl 2020). Yet when vital rate data are available these models provide a powerful means to understand the effects of various ecological disturbances on population growth and simultaneously provide a means to predict how potential restoration strategies may be best used to help sustain these species over time (Hernandez-Pacheco et al. 2011, Bostrom-Einarsson et al. 2018, Edmunds and Riegl 2020). This study uses a combination of size-structured matrix population models, elasticity analyses, and simulation modeling to answer fundamental questions regarding the demographic consequences of disturbance and restoration for *O. franksi*, a dominant reef building coral in the wider Caribbean (Johnston et al. 2016). Through these analyses three questions were assessed:

i) What is the size class structure of an *Orbicella franksi* population during a period with no reported disturbances or restoration efforts?

ii) How do mild and severe disturbances impact size class structure relative to the baseline scenario by the years 2030 and 2050?

iii) Does restoration stabilize populations or offset losses stemming from disturbances?

2. Methods:

2.1. Collection methods:

Vital rate data on individual colonies of *Orbicella franksi* were collected in both East and West Flower Garden Banks from 2011 through 2015 (Figure 1). While the FGB National Marine Sanctuary was established in 1992, average percent coral cover for East and West Flower Garden Banks has been recorded since 1974 (Jackson et al. 2014). East and West FGB are approximately 143.4 km^2 and approximately 1.85 km^2 of that area is coral reef habitat (NOAA 2020). The East and West FGB reefs are at the crest of salt domes in the Gulf of Mexico approximately 180 km from the southwest coast of Texas (Minnery et al. 1985). Empirical data were obtained from Maher et al. (2018) in which a total of 121 *O. franksi* coral colonies were photographed for five years (2011 – 2015), and planar projections were drawn digitally and recorded as a representation of colony area (cm^2). These empirical data were used to estimate annual growth rates of various sized coral colonies. No disturbances were seen to impact these colonies during this time. While coral populations at these reefs are relatively stable and free from disease, in the summer of 2016 a coral mortality event affected parts of East FGB. This disturbance was driven by the effects of floodwaters reaching the area, in conjunction with localized upwelling, ultimately leading to hypoxia (Johnston et al. 2019b, 2019a, Kealoha et al. 2020, Shore et al.

2021). As the oceans continue to warm, it is likely that FGB, like all reefs, will face more frequent and severe threats such as hypoxia and bleaching (Johnston et al. 2019a).

2.2. Matrix Population Modelling

2.2.0 Model Terminology and Construction

Five size classes were chosen incorporating current understanding of the model species (i.e. natural history knowledge regarding growth, survivorship, etc.). Following Carson et al. (2011), the five size classes identified were: small (< 250 cm^2), medium (250-500 cm^2), large (500-1000 cm^2), x-large (1000-2000 cm^2), and xx-large (>2000 cm^2). These size classes are broad enough to capture sufficient variability in annual growth rates, and narrow enough to capture a range of transition probabilities and sampling error (Carson et al. 2011). Transition probabilities are the likelihood a coral will grow or shrink from one size class to another, die, or stay in the same size class from one time point to the next, in this case one year. Ultimately the chosen size classes result in a relatively even number of colonies in each size class comprising the population projection vector. Specifically, the proportion of the population (n = 121) in each size class was derived from the corresponding values in the dominant right eigenvector after the population converged on the stable stage distribution (terms defined below). Matrix population projection models are a subset of demographic models that describe vital rates such as the probability of surviving and remaining in a given age or stage class (Caswell 2001). When the elements in a given population projection matrix describe the probability of growing or shrinking among various age classes within a given period of time (e.g. from age 1 to age 2) they are known as Leslie matrices (Leslie 1945). When probabilities such as in this study describe transitioning from one life stage to another, they are called Lefkovitch matrices (Figure 2; Lefkovich 1965). In corals age doesn't relate to as many biological characteristics as size, and thus for corals a size-based Lefkovitch population projection matrix was developed as in Vardi 2012, Lirman 2003, and others. Using linear algebra, the dominant eigenvalue, and the associated right and left eigenvectors of the population projection matrix can be calculated. From a biological standpoint, the dominant eigenvalue is the finite rate of increase or population growth rate, the right eigenvector is the stable stage distribution or proportion of the population in each size class, and the left eigenvector contains the corresponding reproductive value of each size class (Caswell 2001, Lirman 2003). The population projection vector contains the number of individuals in each of the size classes. When the population projection matrix is multiplied by the population projection vector, it yields the population size in the next time step, and by iterating this process, estimates of the population size, growth rate, and stable stage distribution are generated (Stubben and Milligan 2007).

Using the empirical vital rate data collected from 2011 - 2015, four population projection matrices were created to represent annual changes among size classes from 2011 to 2012, 2012 to 2013, 2013 to 2014, and 2014 to 2015 using the equation

$$n_{t+1} = \mathbf{A} \text{ x } n_t$$

where **A** is the population projection matrix estimated for each time step (i.e., year), n_t is the number of individuals in year *t*, and n_{t+1} is the number of individuals in year t+1. From these four annual population projection matrices (i.e., $\mathbf{A_{01}}$, $\mathbf{A_{12}}$, $\mathbf{A_{23}}$, and $\mathbf{A_{34}}$) a single mean population projection matrix was calculated. This generated a mean (+/- se) value for each of the elements comprising a single population projection matrix spanning the five-year period of time for which empirical vital rate data were available (i.e., from 2011-2015). From this aggregate mean population projection matrix spanning from 2011 to 2015, the long-term population growth rate (i.e., lambda) was calculated. As described above, the dominant right eigenvector of the mean population projection matrix provided estimates of the proportion of the population in each size class. These values were combined with the empirical data describing the actual number of individuals in each size class in 2015 to forecast the total population size annually from 2016 to the year 2050, focusing results and discussion on the population in the years 2030 and 2050.

Elasticity analyses were conducted on the mean population projection matrix to assess the relative importance of the individual vital rates (growth, survivorship) to the population growth rate (i.e. λ). Elasticities measure the proportional sensitivity of λ to proportional perturbations in the individual matrix elements, a_{ij} (Caswell 2001). Elasticity was calculated as:

$$E_{ij} = \frac{a_{ij}}{\lambda} \times S_{ij} \qquad (6)$$

where S_{ij} is the sensitivity matrix. S_{ij} was calculated as:

$$S_{ij} = \frac{v_i w_j}{< w, v >} \qquad (7)$$

where v is the dominant left eigenvector of $\boldsymbol{A}$ (i.e. the reproductive values of each size class), w is the dominant right eigenvector of $\boldsymbol{A}$ (i.e. stable stage distribution or proportion of the population in each of the five size classes), $<w,v>$ is the scalar product of the right and left eigenvectors, v_i is the ith element of v, and w_j is the jth element of w.

Six different scenarios were simulated to forecast size class structures 35 years into the future (equivalent to the year 2050): baseline, mild disturbance, severe disturbance, restoration, mild disturbance with restoration, and severe disturbance with restoration (detailed descriptions below; Table 1). The empirically derived number of individuals in each size class in 2015 was the initial population vector used to simulate future population sizes. To estimate the mean areal coverage of *O. franksi* in the future years, the mean size of individual colonies within each size class in 2015 was calculated from the empirical data. These mean sizes were used to convert number of individual colonies in each size class to areal coverage.

2.2.1. Baseline Scenario:

Using the mean matrix calculated from empirical data, the population size was estimated annually from 2016 - 2050 starting with the number of individuals per size class in 2015 (i.e. the last year empirical data are available; Table 1).

2.2.2. Disturbance Simulation Scenarios:

In order to simulate ecological disturbances on coral reefs of the East and West FGB, two population projection matrices were created to represent two potential disturbance regimes experienced in nature, one mild and one severe. The mild disturbance scenario is representative of a chronic low-level stressor with limited mortality (5%), while the severe disturbance scenario is representative of a large mortality event (25%). Values used in these disturbance scenarios are derived from empirical results found in the primary literature, and all of the disturbance scenarios simulated here are bounded by disturbance-related mortality documented in the same or taxonomically similar coral species inhabiting tropical reef systems (De'Ath et al. 2012, Altieri et al. 2017, Hughes et al. 2018c, Bruno et al. 2019, Johnston et al. 2019b).

The mild disturbance scenario was simulated by perturbing the empirical population data by inducing 20% areal loss and 5% mortality annually (e.g., reducing the size of each individual by 20% and randomly removing 5% of individuals; Table 1). Chronic but relatively mild heat stress or certain diseases could account for the simulated mild disturbance (i.e. these stressors have resulted in 5% mortality and 20% decrease in coral cover; Glynn 1993, Bidegain and Paul-

Pont 2018, Hughes et al. 2018a, Bruno et al. 2019). Individuals that experienced mortality within each size class were randomly selected from the data frame; mortality across size classes was assumed to be similar to estimates from Neal et al. (2017). Cover loss was simulated by artificially reducing the empirical data in 2015 by a given percent and calculating a new 2015-2016 transition matrix, the "disturbance matrix". For example, an individual colony that was 250 cm^2 would be reduced by 20% to 200 cm^2 following a mild disturbance. The population size structure vector from "mild 2016" and the mean "mild disturbance" matrix calculated from the 2015 and 2016 interval was then iterated to simulate an annual chronic disturbance. To explore changes in population size and size structure, the future population stage structure was assessed until the year 2050.

To simulate the severe disturbance, we approximated a hypoxia-related (i.e. low dissolved oxygen) mass coral mortality event that was documented in the East Flower Garden Banks in 2016 (Johnston et al. 2019b). The result of this severe disturbance was a 41% loss of *O. franksi* cover in the affected region (Johnston et al. 2019b). Using this value a severe disturbance year was simulated by decreasing percent cover for all colonies by 40%, and assuming 25% mortality per size class based on *Orbicella* mortality rates documented in Hughes et al. (2018a). The population size structure vector produced from "severe 2016" and the ensuing matrix calculated from the 2015 to 2016 time interval was used to project population size one year into the future following a mass mortality event. This simulates a decrease in both colony size and number of individuals for one year after the severe disturbance. Previous studies of *O. franksi* have shown growth rates following disturbance return to pre-disturbance levels in less than 2 years (Neal et al. 2017). Therefore, following the major disturbance, and based on the frequency of major disturbances in the region, the major disturbance was followed by five years of potential regrowth during a period without major disturbance (Neal et al. 2017, Hughes et al. 2018b, Johnston et al. 2019b). The five-year undisturbed period was simulated by multiplying the population size structure vector following the severe disturbance by the mean population projection matrix derived from the empirical data (2011-2015). Together this simulates a major mortality event followed five years of relatively “normal” (period without major disturbance) growth rates. This severe simulation scenario (one year of disturbance followed by five years of normal growth) was repeated six times through the year 2050 (Table 1). The size class structures were compared against the baseline scenario in 2030 and 2050. However, it should be noted that this scenario could be an underestimation of coral loss due to other disturbances such as SCTLD, as *O. franksi* is highly susceptible to SCTLD and colony losses have been reported as high as 88% following the onset of SCTLD outbreaks in the U.S. Virgin Islands (Muller et al. 2020, Brandt et al. 2021).

2.2.3. Restoration simulation scenario:

The restoration simulation scenario assumes an initial period of growth of microfragments in a nursery (i.e. microfragments of *O. franksi* have been growing for ~3 years and fused prior to outplanting); after fusing, colonies attain the area of a single medium size class individual (~492 cm^2). In the restoration scenario, 30 individual colonies in the medium size class were virtually outplanted each year for six years (Forsman et al. 2015, Page et al. 2018). To simulate these coral restoration efforts, 30 individuals were added to the medium size-class class in the population projection vector for six years beginning in 2019 through 2025. A three-year lag, from 2016 – 2019, was simulated to account for the time it would take to grow the microfragments in a nursery before outplanting. The population stage structure vector was multiplied by the mean matrix from the baseline scenario (i.e. assuming normal growth) to project the population for 25 iterations, from 2025 - 2050. The size class structures from these simulations were compared to the baseline scenario and disturbance scenarios at 2030 and 2050.

2.2.4. Combined restoration and disturbance scenarios

The restoration simulation (i.e. outplanting 30 medium-sized colonies for six years) was combined with both the mild and severe disturbance scenarios as described above. In these combined restoration and disturbance scenarios, 30 individuals were added to the medium size class size vector during the 3rd (2019) through 9th (2024) iterations. In the severe disturbance scenario with restoration, the seventh year (2022) includes a severe disturbance. In this instance the “severe disturbance” matrix described in Section 2.2.2 above is multiplied by a population stage structure vector, with 30 additional medium-size colonies added to the population before the simulated severe disturbance. This iteration of the simulation model assumes the outplanting occurred earlier in the year, and the “severe” disturbance event occurred later that same year (i.e. to capture the probability of a major hypoxic or storm event disturbing the region later in the summer (Johnson et al. 2016, Neal et al. 2017, Hughes et al. 2018b, Bruno et al. 2019, Johnson et al 2019a,b).

3. Results:

3.1. Baseline Scenario:

The empirical data collected from 2011-2015 resulted in a stable population growth rate (lambda = 1.00) with a relatively even distribution of colonies spread among the five size classes (~27 colonies per size class; Figure 3 Table 2). Daily growth rates across all size classes ranged from -0.02 cm^2/day to 0.26 cm^2/day; these translated into annual growth rates ranging from as high as 5031 cm^2/year to as low as -3084 cm^2/year (i.e. some individuals decreased in size). The mean colony size within each of the five size classes (small (< 250 cm^2), medium (250-500 cm^2), large (500-1000 cm^2), x-large (1000-2000 cm^2), and xx-large (>2000 cm^2) was calculated for 2015: small colonies = 167 ± 54 cm^2, medium colonies = 395 ± 78 cm^2, large colonies = 712 ± 167 cm^2, x-large colonies = 1338 ± 222 cm^2, xx-large colonies = 4222 ± 2774 cm^2. Note that the population of *O. franksi* is much larger in the FGB than in other locations in the wider Caribbean (Levitan et al. 2014, Maher et al. 2018). Elasticity analyses reveal the three largest size classes are the three largest contributors to population growth rate (λ), and account for 80% of the rate of change in population size (Table 3). The baseline population projection indicates the size distribution and total abundance of the population would remain stable over time (n = 136 in 2030 and n = 138 in 2050) with a nearly even number of individuals per size class by 2030 (Table 4, Figure 4, Figure 5.1).

3.2. Disturbance Simulation Scenarios:

The mild disturbance simulation resulted in the loss of six individual colonies from 2015 to 2016. The population matrix from 2015 to 2016 (Table 5) was then used to project the population size and size structure to the year 2050. These simulations and elasticity analyses indicated the smallest size class (i.e., colonies < 250 cm^2) was the greatest relative contributors to the population growth rate (elasticity=1.0 i.e., the probability of remaining in the smallest size class). Further, all individuals in the smallest size class remained in the smallest size class (Table 5). Under the mild disturbance scenario, the majority of individuals (91 of 112 individuals) ended up in the small size class by the year 2030, and all but one individual was in the smallest size class by 2050 (114 of 115 individuals; Figure 4; Figure 5.1; Table 4). Furthermore, although there were only 22 fewer individual colonies overall in the mild disturbance scenario compared to the baseline scenario, because all colonies were in the smallest size class, the areal cover was projected to decrease by 90% by the year 2050 under the mild scenario (Figure 5.2 A and C).

A severe disturbance matrix was calculated from 2015 to 2016 (Table 6). The elasticity analysis for severe disturbance also indicated the smallest size class was the greatest relative contributor to population growth rate (elasticity=1.0). Similar to the mild disturbance all individuals in the smallest size class remained in the smallest size class. However additionally, all of the x-large individuals decreased in size to the large size class (Table 6). Only 71 individuals were projected to remain by 2030 and only 31 colonies remain by 2050 (Table 4). The severe disturbance scenario projection had 107 fewer colonies predicted by 2050 and approximately seven times lower areal coverage of coral compared to the baseline scenario (Figure 5.1 and 5.2 A and E).

3.3. Restoration Simulation Scenario:

When restoration was simulated by adding 30 medium size class (i.e., 250-500 cm^2) colonies annually for six years, it resulted in the number of colonies increasing in all size classes, and the total number of colonies increasing from 121 to 267. Also, the colony size distribution in 2050 remained relatively even across the five size classes (Table 4). This simulated restoration scenario increased total coral cover by approximately 50% by the year 2050 (Figure 4; Figure 5.2).

3.4. Combined Disturbance and Restoration Scenarios:

When restoration was simulated (30 medium individuals added annually for six years) along with the mild disturbance scenario there were 297 colonies by 2030 with the majority of individuals in the small size class (231 individuals of 297). The number of individuals was consistent, but by 2050 only two individuals remained in the medium size class and the rest of the individuals were small (295 of 297 individuals; Table 4). Implementing restoration increased areal coverage under the mild disturbance scenario by 160% (Figure 5.2). While there were more individuals in 2050 under the combined mild disturbance and restoration scenario than the restoration scenario with no disturbance, the non-disturbed scenario had 5x more areal coverage due to the mean size of individuals per size class (Figure 5).

The same restoration scenario simulated with severe disturbance resulted in 183 total individuals by 2030 with the majority of colonies in the small size class (n=118). In 2050, 69 individuals remained with about half of the colonies in the small size class (n=35; Figure 4). Restoration increased the areal coverage under the severe disturbance scenario by ~110% in 2050 with half of the areal coverage contributed by xx-large *O. franksi* colonies. However, this was still only 25% of the combined areal coral coverage projected compared to the baseline projection scenario. Estimated areal coverage was almost equivalent comparing the severe and mild disturbance scenarios with restoration, 50,043 cm^2 and 50,439 cm^2 respectively. However, almost all coverage was due to small individuals in the mild disturbance restoration scenario, while the smallest size class contributed only 12% of coral cover in the severe disturbance restoration scenario (Figure 5.2).

4. Discussion:

4.1. Comparing mild and sever scenarios

This study assessed how coral restoration may interact with and potentially offset the effects of mild and severe ecological disturbances. From 2011 to 2015, the *O. franksi* population on the East and West FGB was relatively stable. However, under a simulated mild disturbance scenario, by 2030, 78% of individuals were predicted to be in the small size class and 99% of colonies were projected to be in the small size class by 2050. Populations exhibiting such a downward trend may be headed towards extinction (Riegl et al. 2017). Even though the population is not experiencing a loss of individual colonies under this scenario, their estimated areal coverage greatly decreased over time with or without restoration. However, two times the amount of areal coverage was projected when active coral restoration is implemented. While the number of individuals projected by the year 2050 is higher in the mild disturbance with restoration scenario than in the restoration scenario alone, the areal coverage is approximately six times less. This suggests more frequent restoration may be necessary to combat coral loss in regions that are chronically disturbed. Our findings also indicate that when using a modelling technique that relies on data describing the number of individuals, it is essential to consider colony size distribution as well as areal coverage.

In the severe scenario, five years of normal population dynamics appear to benefit larger individuals and allow the colonies a chance to recover (i.e., increase in size during non-disturbance periods). Compared to the mild disturbance with restoration scenario, the severe disturbance with restoration scenario saw a drastic loss of individuals overall. Furthermore, by the year 2030, 64% of all individuals were small (<250 cm^2). Aerial coverage was projected to be similar in both disturbance with restoration scenarios but almost half of the coral cover in the severe disturbance with restoration scenario was due to xx-large individuals and all individuals in the mild restoration scenario were small. Similar to the mild restoration scenario, hurricanes have been shown promote asexual reproduction through fragmentation mirroring this trend (Foster et al. 2007, 2013). However, if the surviving individuals in the severe disturbance scenarios are larger they may also have the ability to produce more gametes or fragments to create new colonies (Highsmith 1982, Davies et al. 2017); local retention of coral larvae plays an important role in the persistence of coral metapopulations in the FGB (Limer et al. 2020). Under a more severe but less frequent disturbance regime the restoration simulated here appears to enable the population to have a distribution of individuals in each size class more similar to a non-disturbed population. However, the loss of areal coverage due to these simulated severe disturbance events could not be counteracted by the restoration scenario. Number of individuals and areal coverage do not always correlate (Figure 5). Model results suggest more individuals or more frequent outplantings would be necessary to offset either disturbance regime, indicating that restoration is by no means a replacement for preservation, particularly on reefs such as East and West FGB with unusually large colonies. The loss of a few of these large individuals has a disproportionate effect on areal coverage (Figure 5). Ultimately because these corals grow slowly (Groves et al. 2018) disturbance events followed by restoration, are unlikely to replicate the current size distribution.

Under both simulated disturbance scenarios there was a loss of colonies and a shift in the population structure to smaller colonies, both of which result in a loss in projected areal coverage (Figure 5, Table 4). While restoration did provide additional individuals and prevent some coverage loss, the population was still substantially impacted by the disturbances compared to the non-disturbed population projections (Figure 5, Table 4). The *O. franksi* population in FGB was relatively stable from 2011-2015, and there was an even distribution among size classes. When projected to 2050 with no restoration or disturbance events, there was an additional 17 individuals and a slight increase in areal coverage forecasted. However, when even a mild disturbance was simulated annually, the population shifted to mainly small individuals by the year 2030. By 2050, while there were only 16% fewer individuals remaining compared to the baseline projection, the areal coverage was 3.5x less (Figure 5). With sea surface temperatures continuing to rise and disease increasing among many coral populations, severe years of disturbance will likely become more common (Dee et al. 2019, Manzello et al. 2021). In the future, a severe disturbance event could be caused by these increases in temperature, impacts from extreme storms, and/or shifts in the location or areal extent of the Gulf of Mexico dead zone (Rabalais et al. 2002, Turner et al. 2008, Rabalais and Turner 2019).

When comparing mild and severe disturbance scenarios, areal coverage in 2050 is relatively similar, whereas size class structure is not. This discrepancy could be due to annual or "chronic" stress leading to less mortality but many individuals being continually fragmented. Also, this could be a result specific to populations with very extremely large individuals (> 2000 cm^2) such as FGB. This mild scenario could still lead to a loss of the majority of highly reproductive individuals. While the small corals in FGB may be able to retain enough areal coverage to persist over time, the ability to serve as a source population would be jeopardized under either scenario (Davies et al. 2017). Overall, both disturbance scenarios similarly alter which size class contributes the most to population growth rate, from the largest size classes to the smallest size class (elasticity=1.0 small-small transition for both the mild and severe disturbance; Table 3).

4.2. Disturbances in Flower Garden Banks

East and West Flower Garden Banks have had relatively few large disturbances in the past (Jackson et al. 2014). However, disturbances appear to be increasing. From 1972, when the first quantitative benthic assessment occurred, to 1997, three hurricanes impacted the region but only one reported bleaching event occurred (Jackson et al. 2014). In 2005, a coral bleaching event, coral disease event, and two hurricanes affected parts of FGB. From 1998 through 2016 four coral bleaching events were reported, two of which were during years with high hurricane activity (Jackson et al. 2014, Johnston et al. 2019a). Past disturbance events ranged in severity and total coral loss or mortality was not reported or calculated for the majority of disturbances in this region aside from 2016 (Jackson et al. 2014, Davies et al. 2017, Johnston et al. 2019b). Furthermore, disease, ocean warming, and deoxygenation may be compounding increasing the intensity and frequency of disturbances (De'Ath et al. 2012, Hughes et al. 2018b, 2018c, Brandt et al. 2021). Due to these factors, anticipating disturbances is difficult in the region but simulations can be used to elucidate potential size structure shifts of corals following these events. Long term monitoring is crucial to assess demographic shifts and cannot be done with coral cover data alone (Edmunds and Riegl 2020).

Flower Garden Banks has been identified as a possible refugium for *O. franksi* and as a potential source population for lower Caribbean reefs (Davies et al. 2017, Limer et al. 2020). *Orbicella franksi* has been shown to have relatively long pelagic larval durations (PLD) allowing them to seed distant reefs under favorable conditions. However, dispersal can be highly variable and is greatly impacted by disturbances and overall stress (Davies et al. 2017). With climate change shifting currents, PLD may become an important factor in retaining connectivity among reefs (Levin 2006, Davies et al. 2017). The loss of large individuals, which greatly decreases areal coverage, concomitantly decreases the number of gametes produced (Loya et al. 2001, Levitan et al. 2014). Further, massive corals that have bleached or experienced thermal stress have also been shown to produce fewer gametes or have lower fecundity following a disturbance (Levitan et al. 2014, Riegl and Purkis 2015). Our forecasts suggest large individuals that can reproduce via fragmentation and have large areal coverage and thus release more gametes, disappear in the mild disturbance scenario and the number of all individuals decrease in the severe scenario.

Preventing bleaching, disease, and other damage is always the preferred management strategy; however, restoration efforts can be used to help offset some losses. The restoration of massive corals through microfragmentation is becoming more common (Bostrom-Einarsson et al. 2018). By restoring massive species, especially in a source population, multiple reefs can benefit from restoration efforts. Large-scale coral restoration projects such as the Reef Restoration and Adaptation Program in Australia or the Mission Iconic Reefs in the Florida Keys, are propagating massive corals using various propagation methods (e.g., larval, micro-fragmentation). Regardless of methodology chosen for propagation, restoration of massive corals is still experimental. Many variables (e.g., size, density, or genotypic diversity of outplants) can be manipulated, and understanding demography through modeling approaches, such as in this study, is essential to assessing the success of restoration and adapting restoration plans accordingly. Here restoration (not combined with disturbance) increased projected areal coverage by approximately 50%, with the majority of areal coverage being comprised of xx-large individuals. This simulation highlighted how restoration can enhance stable populations and increase individuals across size classes. However, most coral populations do not remain this stable (Downs et al. 2002, Mora et al. 2011, De'Ath et al. 2012). Anticipating how effective restoration is under changing disturbance regimes is important when choosing restoration strategies, as well as how often it needs to occur for certain reefs.

4.3. Modelling demography of corals

Demographic assessments of corals can also be done in regions like the Florida Keys that appear to be increasingly impacted by disturbance events leading to severe loss of cover, and more recent data can be used to determine if certain reefs or areas are more at risk than others. Specifically in the Florida Keys, SCTLD is leading to large losses of coral cover in the lower Caribbean and is difficult to treat (Muller et al. 2020, Brandt et al. 2021). Incorporating demographic assessments such as this one into future studies of SCTLD could elucidate which size classes are most at risk, provide insights into population stability, and quantify how growth rates are affected (Edmunds 2015). Further when attempting to predict and understand the effects of future disturbance intensity and frequency, running multiple scenarios can help “bound the truth” by elucidating the upper and lower bounds of potential impacts. Given that contribution to population growth rate (i.e., elasticity) decreases with size of colony (Table 3), keeping corals in a nursery to enable them to grow into larger size classes before outplanting, should be weighed against the expense of doing so. This is a perennial balancing act that land-based nurseries focused on coral restoration are faced with. Cost of coral reef restoration is highly variable (estimates range 6,000-4,000,000 USD per hectare) and dependent on restoration strategy (Bayraktarov et al. 2019). Research on increasing coral growth in early life stages, may improve the efficiency of restoration using land-based facilities or microfragmentation. By modelling disturbance with restoration in other populations, similarities and differences between populations and species can help highlight which species may be best to restore in certain regions to support reef function and services (Moberg and Rönnbäck 2003, Barbier et al. 2011, Edmunds and Riegl 2020). Projection matrices allow managers to simulate and compare various potential restoration regimes and predict how the current population of corals may respond. This in turn can create more targeted and efficient restoration strategies and lead to more effective management.

Constraints exist with this type of modelling, such as accurately predicting the severity or frequency of future disturbance regimes. Bleaching is a particularly difficult disturbance to model as its effects are not equivalent to coral mortality or cover loss (Hughes et al. 2018c). If colonies are not measured prior to and following an actual disturbance, creating a completely realistic and accurate transition matrix is not possible. Further, disease, extreme storms, and bleaching lead to variable tissue loss as well as mortality (Neal et al. 2017, Hughes et al. 2018c, Muller et al. 2020). In this study size class structure is projected out to 2050 to compare the estimated populations under these two scenarios but within the projection period more variance is likely. Here coral cover is estimated based on the average size of a colony within each size class but, to more accurately predict coral cover, other forecasting methods should be incorporated in future studies (Vercelloni et al. 2020). Furthermore, with respect to coral restoration, and the application of matrix population models, more accurate simulations will require conducting in situ experiments to quantify the response of outplanted corals to disturbances and compare those to both outplanted and "natural" corals in undisturbed regions.

4.4. Future directions

From a biological standpoint, data describing egg reproduction of closely related *O. annularis* exist (e.g. Van Veghel and Bak 1994). However, empirical studies translating these into fecundity or fertility (i.e. fecundity accounting for annual survival), and documenting successful recruitment in situ are incredibly rare (Edmunds 2015). For example, over a 16-year study of *O. annularis* in Jamaica, only one 1 recruit was ever found (Hughes and Tanner 2000). Together the lack of key vital rate data describing the number of offspring produced each year via sexual reproduction of genus *Orbicella* suggest more studies are required on coral recruitment, and together these knowledge gaps contribute to there being no stock-recruitment relationships for any coral species (Holstein et al. 2022). Increased monitoring following disturbances in specific regions for multiple species is the best way to ensure realistic mortality and cover loss are used in simulations. Although obvious, it also bears noting that the more realistic the simulations of the disturbances are and the larger the amount of empirical data, the more realistic the projections of the population will be (Edmunds 2015). Future studies should consider longer term annual sampling from ecologically connected reefs. Eventually this would allow for real disturbances to be captured during sampling events, creating an empirical disturbance matrix that can be projected into the future as well as allow comparisons among populations. Further, long term monitoring following restoration in concert with advancing photogrammetry, would be helpful for creating additional population projection matrices and increasing the accuracy of projections that can be used to project how restored individuals will grow into the future (Dee et al. 2019).

Multiple species of reef building corals are considered threatened, with some populations specifically at risk of extinction such as those in the Florida Keys (Mora et al. 2011, National Marine Fisheries Service 2016, Page et al. 2018). As corals continue to be impacted by disturbances and repaired by restoration, determining how restored communities grow differently than natural communities especially under dynamic disturbance regimes will be important to verify the best restoration strategies (Bostrom-Einarsson et al. 2018, Page et al. 2018). Assessing the demography of multiple species of reef building corals in a region can help guide which species are best to restore (Edmunds and Riegl 2020). Furthermore, it can help highlight how corals are adapting (or not adapting) to shifts in the environment (Riegl and Purkis 2015, Hughes et al. 2018c, Bruno et al. 2019, Nelson and Altieri 2019, Kodera et al. 2020). Other studies have highlighted the impacts of disturbance on reef building corals and also found a general decrease in colony size that could potentially lead to demographic bottlenecks and other negative effects in addition to coral cover loss (Hernandez-Pacheco et al. 2011, Brandt et al. 2013, Pisapia et al. 2020). Mortality among smaller size classes may also be higher in subsequent years or with increasing disturbance frequency and may not be apparent in coral cover surveys alone (Hernandez-Pacheco et al. 2011, Vardi et al. 2012). Simulations using empirical data following both disturbance and restoration events are necessary to create more realistic projections. Integrating matrix population models, with complementary modelling approaches such as species distribution modelling, biophysical modelling of larval dispersal, and structural equation models could elucidate shifts in connectivity and identify sites serving as source or sink populations, providing a deeper understanding of species persistence (Davies et al. 2017, Lewis et al. 2021b), and how changes in the environment are impacting shallow coral population dynamics (Guisan and Thuiller 2005, Foden et al. 2013, Rodríguez et al. 2019, Edmunds and Riegl 2020).

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Figures and Tables:

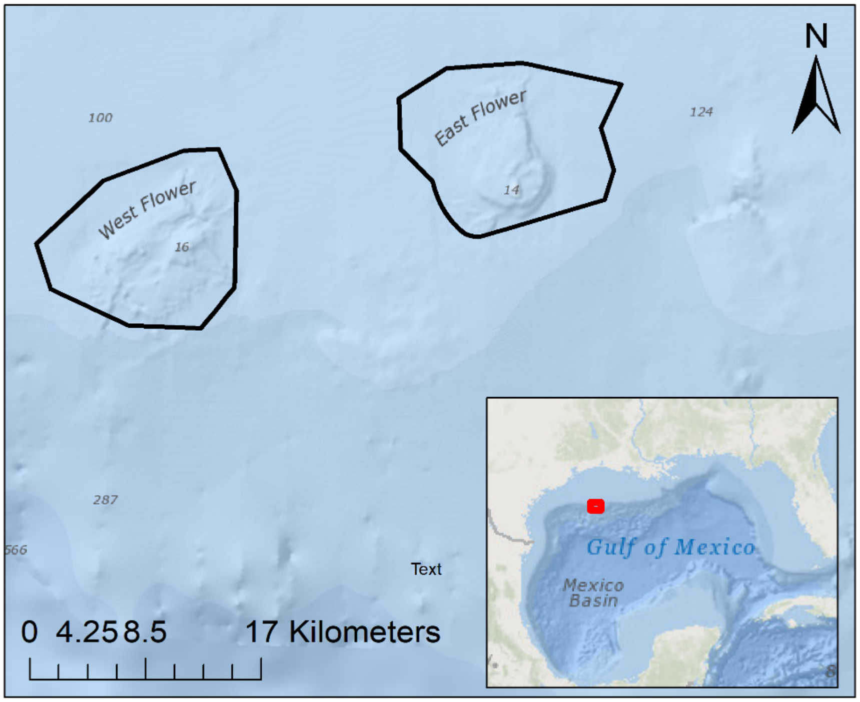
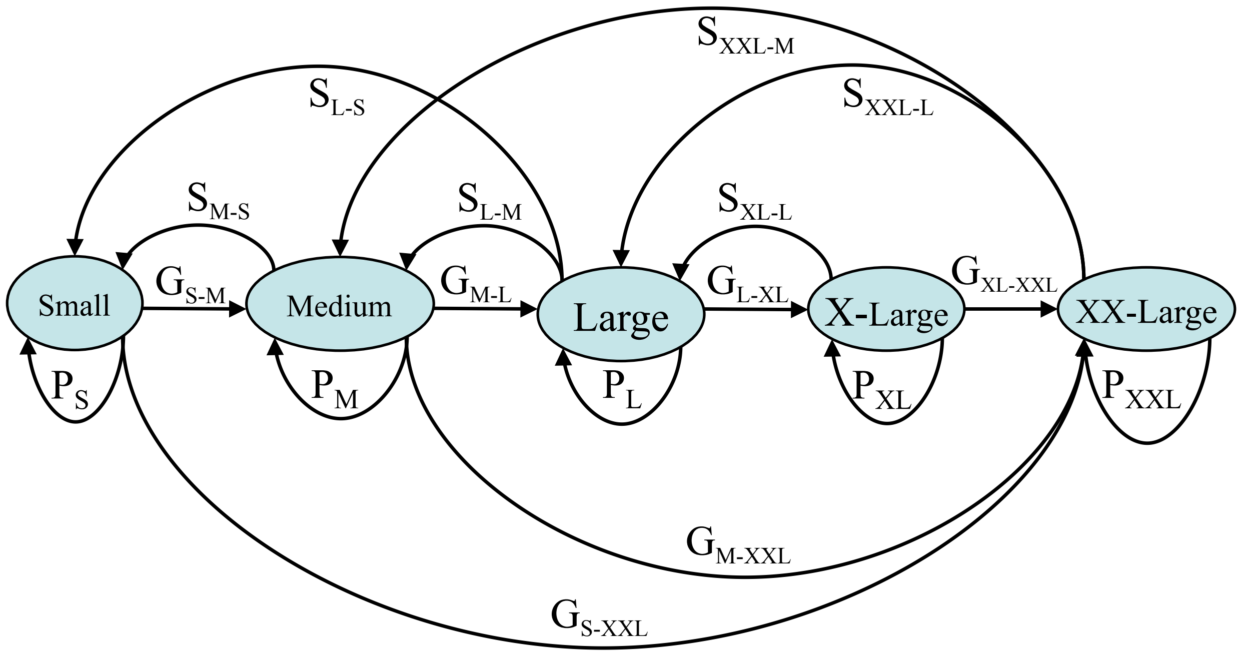


Figure 1:Map of East and West Flower Garden Banks located in the Gulf of Mexico off the coast of Texas.



P_S	$S_{M\text{-}S}$	$S_{L\text{-}S}$	0	0
$G_{S\text{-}M}$	P_M	$S_{L\text{-}M}$	0	$S_{XXL\text{-}M}$
0	$G_{M\text{-}L}$	P_L	$S_{XL\text{-}L}$	$S_{XXL\text{-}L}$
0	0	$G_{L\text{-}XL}$	P_{XL}	$S_{XXL\text{-}XL}$
$G_{S\text{-}XXL}$	$G_{M\text{-}XXL}$	0	$G_{XL\text{-}XXL}$	P_{XXL}

Figure 2. Life cycle diagram (above) and corresponding population projection matrix (below) for *O. franksi* derived from empirical vital rate data collected from 2011 – 2015. Transition probabilities among the five size classes represent the probability of surviving and remaining in the same size class (P), the probability of surviving and growing into a larger size class (G), and the probability of surviving but shrinking into a smaller size class (S).

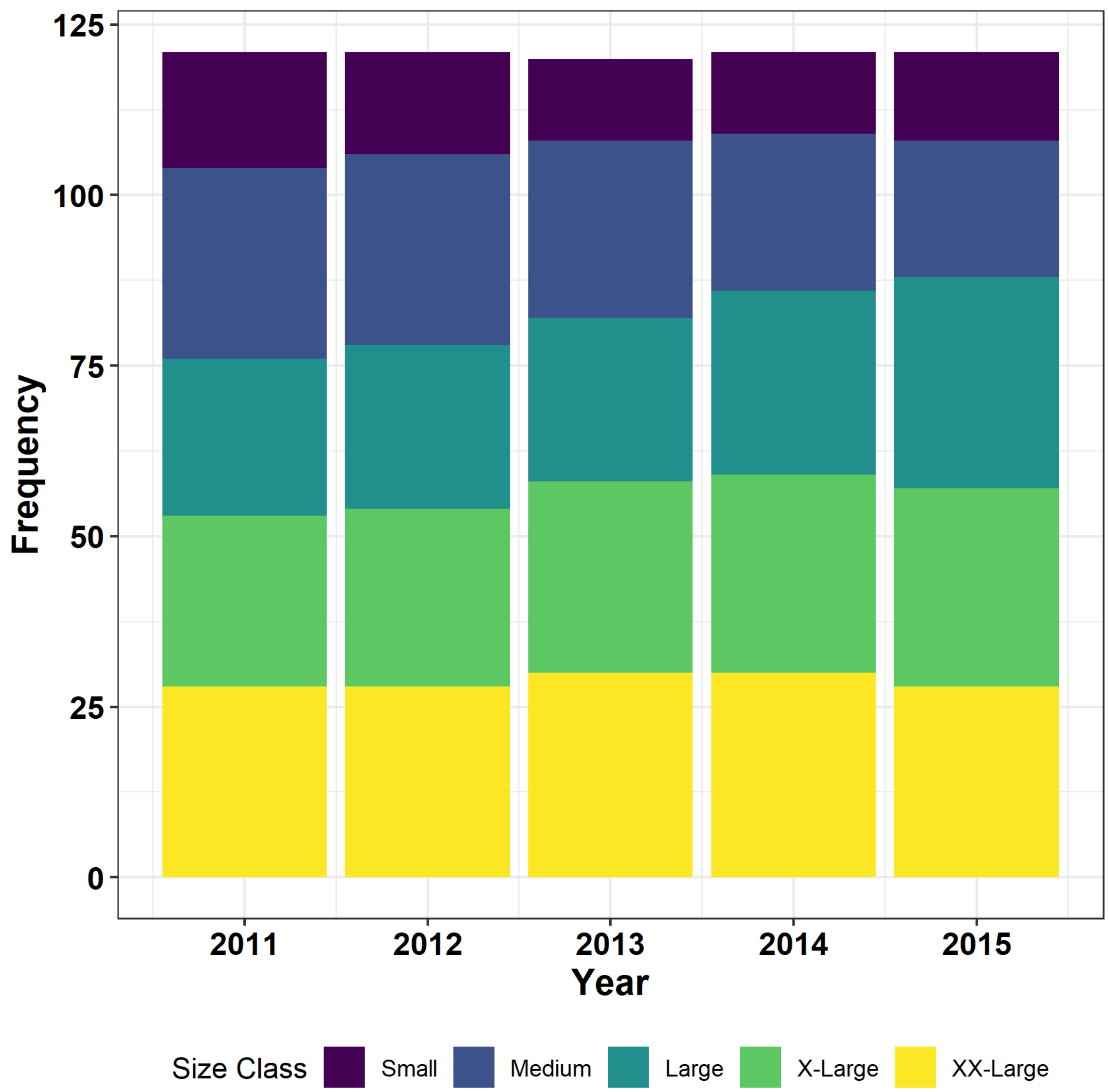


Figure 3: Distribution of size classes from 2011-2015 from East and West Flower Garden Banks. 121 colonies were observed over the five years except when only 120 individuals were observed in 2013. The five colors correspond to the number of colonies in each of the five size classes

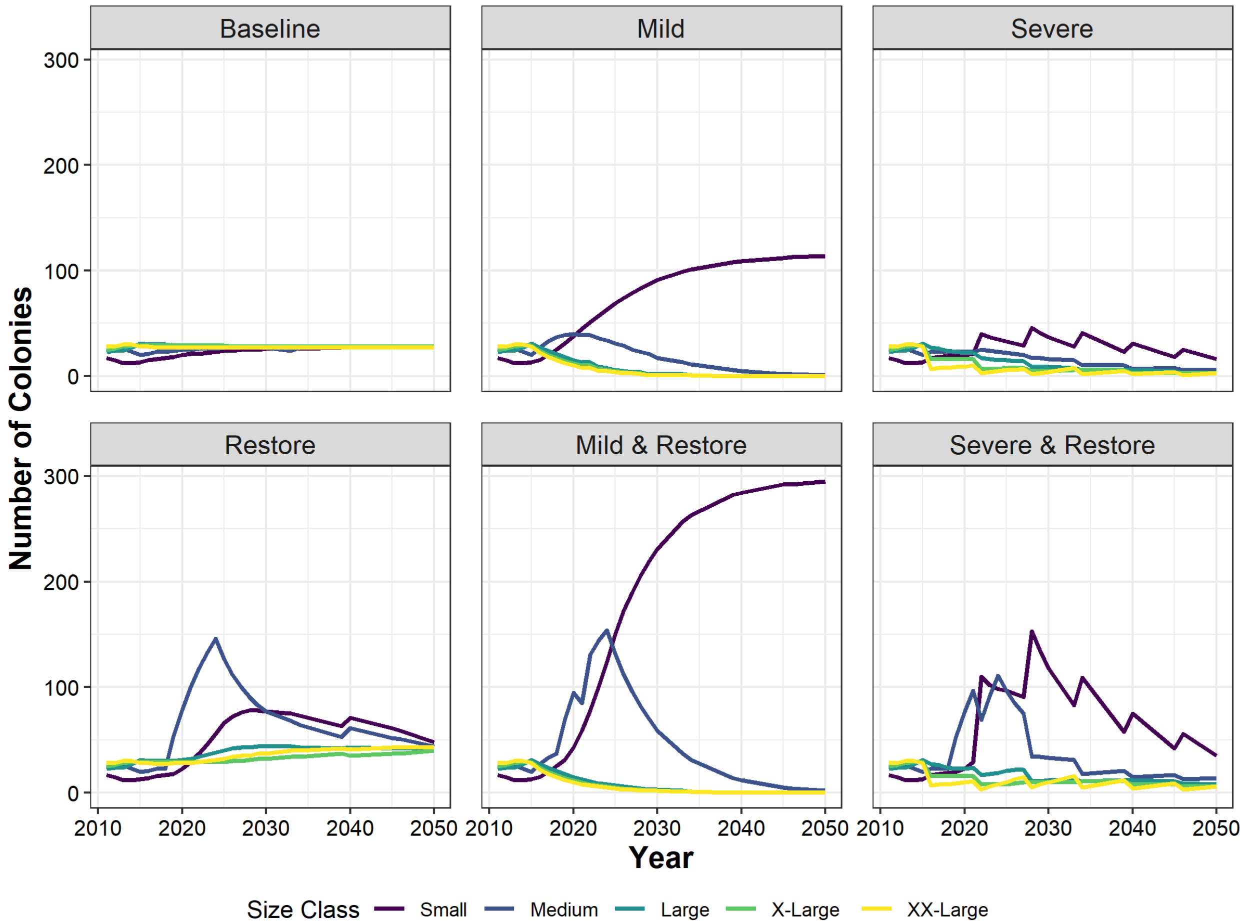


Figure 4: Numbers of *O. franksi* colonies per size class over time under each scenario. The five colors correspond to the number of colonies in each of the five size classes. Panels are labeled by scenario.

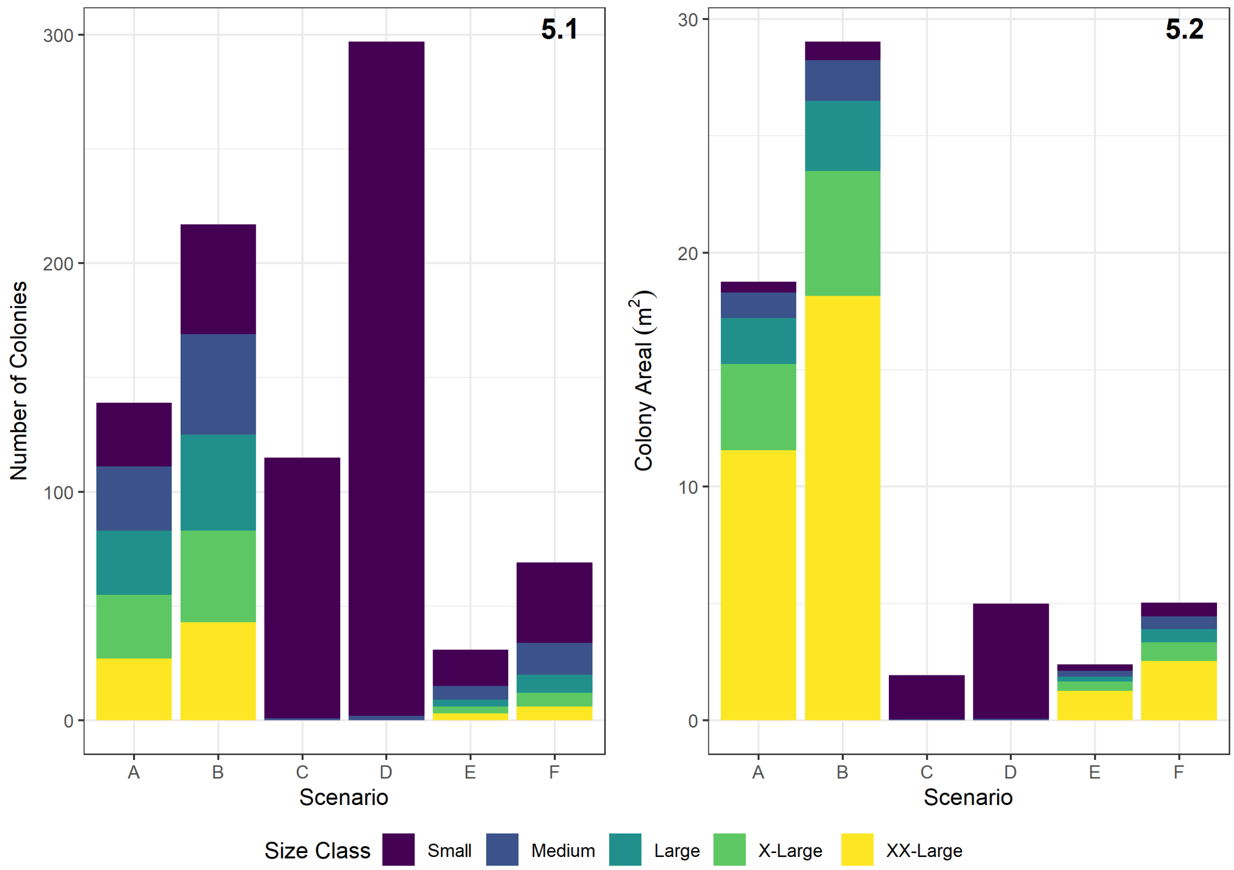


Figure 5. Figure 5.1: Number of individuals per size class projected in 2050 under each scenario. A) baseline scenario: n=138; B) restoration scenario: n=217; C) mild disturbance: n=115; D) mild disturbance and restoration: n=297; E) severe disturbance: n=31 F) severe disturbance and restoration: n=69.

Figure 5.2: Projected areal coverage (m^2) of individuals per size class using mean area of each size class from 2015.

Table 1: Explanation of restoration and disturbance scenarios.

	Percent Decrease of Cover	Percent Mortality	Frequency of Disturbance	Disturbance Years	# Of individuals added
Baseline	0	0	0	none	0
Mild Disturbance	20	5	annually	2016-2050	0
Severe Disturbance	40	25	6 years	2016, 2022, 2028, 2034,2040,2046	0
Restoration	0	0	0	none	30 medium-sized individuals annually 2019-2024
Restoration and Mild Disturbance	20	5	annually	2016-2050	30 medium-sized individuals annually 2019-2024
Restoration and Severe Disturbance	40	25	6 years	2016, 2022, 2028, 2034,2040,2046	30 medium-sized individuals annually 2019-2024

Table 2: Mean population matrix calculated using empirical data from 2011-2015 for baseline projection, lambda=1.00. Values represent transition probabilities between size classes, the values in parentheses represent the standard error, NAN are non-values.

	Small	Medium	Large	X-Large	XX-Large
Small	0.84 (0.05)	0.12 (0.04)	0.04 (0.02)	0 (NAN)	0 (NAN)
Medium	0.03 (0.01)	0.82 (0.02)	0.14 (0.02)	0 (NAN)	0.01 (0.01)
Large	0 (NAN)	0.03 (0.01)	0.87 (0.02)	0.08 (0.02)	0.02 (0.01)
X-Large	0 (NAN)	0 (NAN)	0.04 (0.02)	0.93 (0.02)	0.04 (0.02)
XX-Large	0.02 (0.01)	0.01 (0.01)	0 (NAN)	0.03 (0.02)	0.94 (0.02)

Table 3: Elasticity matrix derived from empirical data 2011-2015.

	Small	Medium	Large	X-Large	XX-Large
Small	0.04	0.01	0.00	0.00	0.00
Medium	0.00	0.07	0.01	0.00	0.00
Large	0.00	0.01	0.17	0.02	0.00
X-Large	0.00	0.00	0.01	0.34	0.01
XX-Large	0.01	0.00	0.00	0.01	0.29

Table 4: 2030 and 2050 size class distributions by projection scenarios.

Size Class	Baseline	Restoration	Mild Disturbance	Mild Disturbance and Restoration	Severe Disturbance	Severe Disturbance and Restoration
2030						
Small (<250 cm^2)	26	77	91	231	37	118
Medium (250-500 cm^2)	27	77	17	59	16	33
Large (500-1000 cm^2)	28	44	2	3	9	12
X-large (1000-2000 cm^2)	28	32	1	2	5	10
XX-Large (>2000 cm^2)	27	37	1	2	4	10
Total:	**136**	**267**	**112**	**297**	**71**	**183**
2050						
Small (<250 cm^2)	28	48	114	295	16	35
Medium (250-500 cm^2)	28	44	1	2	6	14
Large (500-1000 cm^2)	28	42	0	0	3	8
X-large (1000-2000 cm^2)	28	40	0	0	3	6
XX-Large (>2000 cm^2)	27	43	0	0	3	6
Total:	**138**	**217**	**115**	**297**	**31**	**69**

Table 5: The "mild disturbance" matrix was developed to simulate a 20% decrease in coral cover and a 5% increase in mortality across all size classes, from one year to the next. It was based on data from 2015.

	Small	Medium	Large	X-Large	XX-Large
Small	1	0.17	0	0	0
Medium	0	0.83	0.4	0	0
Large	0	0	0.57	0.36	0
X-Large	0	0	0.03	0.61	0.22
XX-Large	0	0	0	0.036	0.78

Table 6: The "severe disturbance" matrix was developed to simulate a decrease in coral cover by 40%, and a 25% increase in mortality across all size classes, from one year to the next. It was based on data from 2015. In the simulated disturbance scenarios, this matrix was used to project the population size and distribution one year into the future, every six years.

	Small	Medium	Large	X-Large	XX-Large
Small	1	0.83	0	0	0
Medium	0	0.17	0.95	0	0
Large	0	0	0.05	1	0
X-Large	0	0	0	0	0.70
XX-Large	0	0	0	0	0.31

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