RESTORATION RENAISSANCE: CHARTING THE COURSE FOR CORAL RESTORATION DECISIONS

BY

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Abstract

The science, policy, economics, and outcomes associated with coral restoration can benefit from modeling approaches that efficiently measure — and can maximize — coral reef recovery and resilience. Integral Projection Models (IPM) are a powerful tool to identify critical life stages and transitions that can maintain or improve populations exposed to increasing local and global stressors. This study built an IPM to understand the population dynamics of *Acropora* corals that are essential for reef habitat and structure, but also highly sensitive to stressors. The model was calibrated using 20 years of population data from the 8m reef slopes of a representative Pacific Island, Saipan, Commonwealth of the Northern Mariana Islands. These data and literature sources were used to quantify the three key components of the IPM - survival, growth, and fecundity. The calibrated model predicted that 12 - 148 cm^2 (post-recruit) corals were most sensitive to the stressors currently affecting *Acropora* (e.g., bleaching), suggesting that post-settlement mortality may be more influential compared to recruitment limitation. To validate and forecast these findings under varying restoration scenarios, the IPM was translated into a discrete model that predicted the coverage and size-distributions of *Acropora* at annual intervals. The discrete model reliably predicted observed *Acropora* cover and size distributions across a 20-year projection. Building upon this calibrated foundation, two restoration scenarios were simulated at varying intensities: recruit enhancement and adult enhancement. Both scenarios added corals annually over a span of 20 years and the model was iterated for 100 simulations. Adult enhancement revealed a significant increase in reef coverage and size structure over the 20-year span. For instance, adding just one adult coral colony each year to the simulated coral plots (0.25 corals/m^2), by year 20, the coverage increased from 3% (no restoration model) to 51% (adult enhancement). By comparison, recruit enhancement scenarios did not differ significantly from the base population model in terms of coverage and the size structure shifted toward smaller corals. In addition to revealing inherent growth rate and critical size class parameters, the IPM predicted the prevalence of post settlement mortality and, therefore, the enhanced success of the adult enhancement approach compared to recruit enhancement.

In order to restore 15.5 m^2 of reef, the former would require outplanting ten 30 cm diameter corals (~700 cm^2) annually for 20 years. Disentangling population dynamics, this study represents an early attempt to model restoration scenarios; more importantly, it introduces a foundational framework for more expansive modeling to holistically enhance future restoration approaches and decision-making.

Keywords: *coral restoration, Integral Program Model, computer model, population ecology*

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Introduction

Coral reefs span the coastlines of over 100 countries, support 5% of global biodiversity (Reaka-Kudla et al., 1997; Souter et al., 2021) and provide essential services to ecosystems and human societies. The value of these global services is estimated to be $2.7 trillion per year; tourism alone accounts for $36 billion (Souter et al., 2021). Yet, over the past 50 years, live coral coverage has declined globally by 50% (Eddy et al., 2021). Climate change impacts can include heat stress, higher-intensity tropical storms, and even crown-of-thorns starfish outbreaks that cause increased mortality and reduced cover on coral reefs. Population outbreaks of crown-of-thorns starfish (CoTS, *Acanthaster* spp.) in the Indo-Pacific are a major threat to coral reefs. A single CoTS can consume live coral at a destructive rate of 4 – 13 m^2 per year (Dixon, 1996). Climate change related impacts are outpacing the natural rate of both coral evolution and coral thermal tolerance adaptation (van Oppen et al., 2017).

Further compounding climate change and acute stress events, local stressors (e.g., overfishing, pollution, and tourism) provide lower-level chronic stress to coral reefs. While slowly reducing coral cover, the real impact of local stressors is a slowed or lack of recovery following acute events. Indirect stressors caused by increased rainfall can lead to increased runoff, nutrients, and turbidity, and decreased salinity (Haapkylä et al., 2013; Perry et al., 2014), all with potential links to coral diseases (Redding et al. 2013; Lamb et al., 2018) and macroalgal blooms inhibiting coral recruitment (Kuffner et al., 2006; Doropoulos et al., 2014).

To combat global ecosystem decline, the United Nations declared this decade to be the “Decade on Ecosystem Restoration” (IUCN, 2022) and in doing so established the 17 Sustainable Development Goals to combat climate change and improve the resilience of ecosystems and communities that rely on them (United Nations General Assembly, 2015). Ecological restoration is defined as the "process of assisting the recovery of an ecosystem that has been degraded, damaged, or destroyed" (SER, 2004). The International Coral Reef Society published a plan to save coral reefs, advocating three equally important pillars for success: mitigation of carbon dioxide emissions, mitigation of local pollution, and active restoration (Knowlton et al., 2021). Restoration has emerged as a viable method for rehabilitating ecosystems including salt marshes, mangroves, and seagrasses at local scales (Young et al., 2012; Shaver & Silliman, 2017), but not as a solution for regional or global scales. Coral reef restoration, a nascent field, is in urgent need of development and rigorous evaluation of available techniques.

In the last decade, restoration managers and practitioners have reported $258 million invested in various coral restoration efforts across 56 countries (Hein & Staub, 2021). Individual restoration projects can range from $11,717 to $2,879,773 per hectare (Bayraktarov et al., 2015). One concern is the high cost of restoration may outweigh potential benefits and alternative investments (Spurgeon, 2001; De Groot et al., 2013). Restoration ecology is a maturing discipline with few long-term studies to document the fate of restored corals. A review by Boström-Einarsson (2020) found coral restoration studies to be dominated by short-term projects – 60% of projects reported monitoring for less than 18 months. This is problematic because short-term restoration successes frequently do not translate into long-term sustained recovery (Søndergaard et al., 2007; McCrackin et al., 2017). Without addressing the causes leading to coral decline, restoration may not be enough.

Restoration decisions must be based on local conditions, coral species life histories, material availability, cost, and a clearly defined restoration objective (Boström-Einarsson et al., 2020). A 2017 literature review identified six common restoration objectives: (1) accelerate reef recovery post-disturbance, (2) re-establish a self-sustaining, functioning reef ecosystem, (3) mitigate anticipated coral loss prior to a known disturbance, (4) reduce population declines and ecosystem degradation, (5) provide alternative, sustainable livelihood opportunities, and (6) promote coral reef conservation stewardship (Hein et al., 2017). To improve restoration of coral reefs, efforts must not be undertaken solely as technical tasks; rather, they must holistically, collaboratively, and innovatively integrate scientific knowledge with social and policy concerns (Baker & Eckerber, 2013). With clear goals, restoration can be designed to improve the future of restoration ecology. The development and application of computer modeling has potential to fill the present gaps in knowledge (some due to a lack in long-term monitoring) and help design and evaluate differing restoration approaches.

Modeling is a powerful tool that should be leveraged to better comprehend the complexity and interaction of climate change, local stressors, and their influence on restoration; integrate and analyze large data sets (Arías-González et al., 2022). This allows prediction of coral growth and survival when exposed to a wide range of climate-induced and local stressors. Given the global increase in coral-reef monitoring programs that have been tracking reefs through time, several studies have developed models to accurately predict coral cover and size distributions through time (Kayal et al., 2019; Edmunds et al., 2014; Shlesinger and Van Woesik, 2021). This study builds upon previous studies to create a model that predicts survival, growth, and recruitment, and then applies the calibrated model to several restoration scenarios. To date, few studies have harnessed the power of population modeling and size classification modeling as they apply to coral growth and restoration (Benjamin et al., 2017; Lirman and Miller, 2003). To address this knowledge gap, this study presents a population model that simulated several common restoration scenarios to evaluate their potential strengths and weaknesses in mitigating the decline in coral populations in the face of climate change.

Methods

This study used long-term coral-reef monitoring data from the Commonwealth of the Northern Mariana Islands (CNMI) to calibrate a coral size-and-growth model that was then used to evaluate two different restoration approaches with varying intensity. Since 2003, the CNMI Bureau of Environmental and Coastal Quality (BECQ) Coral Reef Monitoring Program has collected coral population demography data as part of a broader long term monitoring effort across Micronesia. Data were collected from fifteen sites around Saipan island representing varying reef types, wave exposure, watershed influence, and management regimes (Figure 3). At each site, 5 x 50 m transects were laid at the 8-10 m contour, and 0.5 x 0.5 m^2 quadrats were placed at equal intervals. Within each quadrat, the taxonomy and size of each coral colony whose center point lands inside the frame were recorded. For colony size metrics, the maximum diameter and the diameter perpendicular to the maximum were recorded (Houk and van Woesik, 2010). This provided species-level demographic data across 15 sites over 20 years, collected annually or every two years. The present model was based on *Acropora* corals found on the outer reefs that have been declining due to increased frequencies of climate-induced stress events (n=8 sites, Figure 3).

Across worldwide restoration projects, 30% of studies have used *Acropora* corals due to their status on the IUCN Red List of Endangered Species, ecological importance, susceptibility to climate-induced disturbances, and fast growth (Boström-Einarsson et al., 2020). In total, 31 *Acropora* species have been recorded across the eight outer reef Saipan sites since 2003. Nearly all (26/31) of these species have digitate/corymbose growth forms. Herein, all digitate/corymbose species were binned together for assessment and modeling. Coral colony size vectors were averaged for each site-year, then averaged across sites for each year to reveal island-year aggregation to develop size-frequency histograms and estimates of percent coral cover that were used to inform and evaluate the models described below. The percent coverage is scaled to 4 m^2 – the area of a single transect (16 x 0.25m^2 quadrats on a single transect).

Integral Projection Model

An Integral Projection Model (IPM) was used to depict the percent cover, demography, and most influential size-classes of *Acropora* corals to sustain populations under varying scenarios. The IPM was first introduced by Easterling, Ellner, and Dixon (2000) as an alternative to matrix projection models for populations with continuous sizes or states. IPMs are a powerful tool to quantify the influence of population demography from three key attributes: survival, growth, and fecundity. Together, these three calibrated attributes can be used to forecast population growth, survival, and demography into the future. The core of the IPM is the *kernel*, a function describing how the state of an individual at time *t* dictates its state and its offspring's state at a future time *t+1*. The IPM uses vital rate data (survival, growth, and fecundity) to forecast population dynamics and assess the most critical size range(s) associated with each population state. The vector of coral colony sizes is multiplied by the dominant eigenvalue associated with the vital rate data to produce a projection of sizes into the future (Easterling, Ellner, and Dixon, 2000). Eigenvalues are scalar quantities derived from population models that define the population's growth rate. A dominant eigenvalue greater than 1 suggests exponential population growth, while a dominant eigenvalue less than 1 indicates decline towards extinction. The computational framework for this study is based on numerous studies that have introduced and applied IPMs to coral reefs (Shlesinger and van Woesik, 2021; Kayal et al., 2019; Edmunds et al., 2014). Input values of colony diameters were transformed to areas assuming that corals were elliptical in nature ($\boldsymbol{\pi} \times r^2$). These areas were log transformed to linearly match their relationship with vital rates, or for matching units. These vital rates comprise growth, survival, and fecundity. Each coral colony passed through a kernel that calculated these vital rates.

Growth

Estimates of *Acropora* growth were obtained from the CNMI data sets. Noted above, mean colony sizes were calculated for each site-year, then differences in sizes were calculated between consecutive years to produce a growth rate (cm^2/year). Site-based growth rates were averaged across the representative outer reefs at the island scale, with standard deviations carried across all levels of aggregations. This resulted in average (+/- SD) growth rates for each year.

Two approaches were used to determine growth rates for IPM modeling: (1) a non-disturbance growth rate associated with field data that didn't include disturbance years and (2) a net growth rate inclusive of all years including disturbances. The non-disturbance growth rate placed an emphasis on the inherent capacity for coral growth, while the net growth represented growth while being exposed to modern disturbance regimes. Three significant disturbance events occurred since 2003: (1) major COTS outbreaks between 2004 and 2006, (2) minor COTS outbreaks between 2010-2011, and (3) major bleaching between 2016 and 2017. Raw data were bootstrapped to produce 100 simulations of growth rates and their associated standard deviations and standard errors. Growth rates for both disturbance and non-disturbance scenarios represented inputs to the continuous version of the IPM and the non-disturbance scenario was input to discrete versions of the IPM.

Survival

A study by Madin et al. (2014) examined size-dependent mortality between different growth forms of coral. The study found growth form to be a better predictor of yearly mortality than species, thus supporting this study's justification for grouping *Acropora* species represented by digitate and corymbose growth forms. Using the mortality curves from this study as a guide, a survival binomial distribution was generated with a switchpoint between 25 and 184 cm^2 (switchpoint between corals with a geometric diameter between ~5.5 cm and ~15 cm) (identified from Madin et al.). From this binomial distribution, the survival slope and intercept were extracted to be used in the IPM kernel predicting size-specific survival probabilities.

Fecundity

Fecundity was calculated as the product of i) the probability that a colony is reproductive as a function of colony size, ii) the proportion of reproductive polyps within a colony as a function of colony size, and iii) the potential maximum number of oocytes produced as a function of colony size (Shlesinger and van Woesik, 2021). Functions for these relationships were pulled from literature based upon previous studies described below.

Acropora studies have revealed a range of ages and sizes for different species reaching sexual maturity, with sizes ranging from 12.3 cm to 30 cm (Table 1). Given this broad range of *Acropora* sexually mature sizes, a diameter of $\geq$15 cm (176.7146 cm^2) was used as the threshold for defining potentially fecund corals. To determine the probability that a colony is reproductive, a binomial distribution was built where the probability of a colony being fecund when greater than or equal to 176.7146 cm^2 is 95%, thereby taking into consideration possible variation at the lower sizes. This distribution was modeled using a binomial regression with a logit link.

Table 1. Adapted from Ligson and Cabaitan (2021) summarizing the minimum diameters of sexually mature *Acropora* species.

Species	**Diameter at Sexual Maturity**	**Reference**
Acropora tenuis	12.5 – 20 cm	Iwao et al., 2010; dela Cruz and Harrison, 2017
Acropora millepora	12.3 cm	Baria et al., 2012
Acropora palmata	30 cm	Chamberland et al., 2016

A study by Rapuano et al. (2023) examined sexual maturity in five different species of coral. Among these species, the study recorded the proportion of reproductive polyps in large and small fragments on *Acropora hyacinthus*. While Acropora hyacinthus is a tabular coral, Madin et al. (2014) demonstrated similar traits between morphologically similar growth forms. In particular, tabular acroporids share a nearly identical mortality curve to corymbose acroporids. For this reason, the assumption of the proportion of reproductive polyps is made from tabular coral data. Pulling from Rapuano et al.'s (2023) supplemental data, the large and small proportions of reproductive polyps were averaged and used to build a dataset with 176.7146 cm^2 as the turning point of reproductive potential with a maximum possible proportion of 74%. This data was used to build another binomial regression to pull the slope and intercept to be used in the fecundity calculation.

To determine the number of oocytes as a function of colony size, morphological fecundity values were pulled from Alvarez-Noriega et al. (2016) where they examined corymbose (*A. nasuta* and *A. spathulata*) and digitate (*A. humilis* and *A. cf. digitifera*) *Acropora* from 2009 to 2013 on Lizard Island in the Northern Great Barrier Reef. Alvarez-Noriega et al. calculated the number of oocytes per colony as the product of the probability of a polyp being fecund, the number of oocytes per fecund polyp, and the number of fecund polyps in the colony. The number of oocytes as a function of colony size were pulled from Alvarez-Noriega et al.'s figure using WebPlotDigitizer to digitally extract the x and y values from the figure JPEG (Alvarez-Noriega et al., 2016, Figure 2 D; Rohatgi, 2022). These values were used in a negative binomial regression to generate the slope and intercept for the function described by Shlesinger and van Woesik (2021).

Establishment probability and IPM predictions

Once the IPM is informed with survival, growth, and fecundity, it can predict the fate of all existing colonies. However, the IPM also predicts the establishment of new recruits based on the fecundity and reproduction kernels. Not all coral larvae will survive to become new recruits and one last static parameter is needed to define the probability that a new recruit will survive and enter the population. Shlesinger and van Woesik (2021) defined establishment probability as the ratio of recruits observed in time *t+1* compared to the number of potential oocytes produced in time *t*. To calibrate the establishment probability, the IPM linear equation to determine the number of oocytes was then multiplied by different probabilities until the result produced the desired number of settled larvae to represent the number of recruits found on the reefs of Saipan. Shlesinger's and van Woesik's (2021) establishment probability served as the starting point and kept increasing at even intervals until an establishment probability of 3.877751e-15 was reached producing the desired number of recruits.

New recruits were given a randomly generated size based on long-term data with a max size of 5-cm diameter (19.63495 cm^2). All sizes generated less than 1-cm diameter were removed according to Preston's Veil Line theory (Preston, 1948) as corals sampled at this size are not visible to surveyors and thus rarely sampled.

Integral Projection Model - Kernel

The integral projection model was constructed using size-dependent survival, growth, and reproduction functions to estimate the overall population growth rate. Table 2 summarizes the equations used in the kernel formulation and calculation.

Table 2. Summary and description of the equations used in the Integral Projection Model.

Equation		Description
General Mathematical Form of IPM	$n(z', t+1) = \int_{Lower}^{Upper} K(z', z) n(z, t) dz$	**z'**= colony size at t+1 **z**= colony size at t **n(z', t+1)**=size distribution estimated as a function colony size distribution at t+1 **n(z, t)**=size distribution estimated as a function colony size distribution at t **K(z', z)**=kernel relating colony size distribution at t to t+1 using survival, growth, and reproduction functions
Kernel	$K(z', z) = s(z) g(z', z) + r(z', z)$	**s(z)**=survival **g(z', z)**=growth **r(z', z)**=reproduction and recruitment
Reproduction Sub-Kernel	$r(z', z) = P_{colony}(z) P_{polyps}(z) f_{oocytes}(z) f_{recruits}(z') P_{establishment\ ratio}$	$\mathbf{P}_{colony}\mathbf{(z)}$=probability that a colony is reproductive as a function of colony size $\mathbf{P}_{polups}\mathbf{(z)}$=proportion of reproductive polyps within colony as a function of colony size $\mathbf{f}_{oocytes}\mathbf{(z)}$=potential maximum number of oocytes as a function of colony size $\mathbf{f}_{recruits}\mathbf{(z')}$=size distribution of recruits at t+1 $\mathbf{P}_{establishment\ ratios}\mathbf{(z)}$=ratio of recruits observed at t+1 compared to potential oocytes at t

The IPM was built using a grid of 500 mesh points and discretized into upper and lower limits (7.458 and -0.217 on a logarithmic scale). Elasticity and sensitivity analyses were conducted to determine the contribution of demographic processes and colony size transitions to population growth rates and stability (Shlesinger and van Woesik, 2021). Sensitivity analysis examines which size class has the greatest impact on the model output. Elasticity analysis is another type of sensitivity analysis that measures the proportional change in population growth rate in response to a proportional change in a vital rate. This helps to identify which vital rate has the greatest impact and which size class is most sensitive to changes in vital rates.

Population Projections Using a Discrete Growth Model

To predict the percent cover and size-class distribution at each time step into the future, a discrete model was generated informed by the IPM. The same vital rates described above were applied to each sequential vector of colony sizes, and the outcomes were populated into an output matrix. One-hundred simulations of the discrete model were run that each projected the population 20 years into the future. In sum, each year builds upon the previous year continually looping through the data pulling from survival, growth and fecundity variables (Figure 1). To take into account disturbance within the loop, each year had a one in five chance of experiencing a disturbance. The disturbance could range anywhere from a 30-75% loss of coral. These values were based on regional observations over the past two decades for Guam and Saipan (Houk et al., 2014; Raymundo et al., 2019).

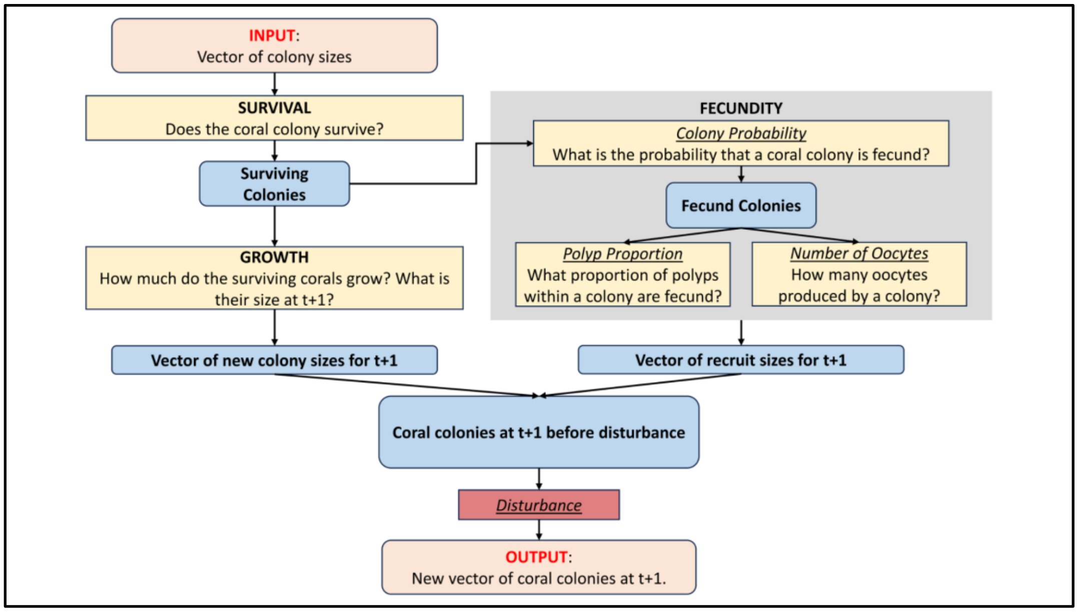

Figure 1. **Flowchart of the model.** This represents the path each individual coral takes in each iteration of the model and how the model determines coral survival, growth, and fecundity in one years' time.

Restoration Scenarios

Two restoration scenarios were tested – each with different quantities and sizes of corals outplanted. These scenarios include (1) recruit enhancement outplanting high quantities of small corals ranging from ~1 cm to ~2 cm diameter, and (2) adult enhancement outplanting small quantities of large corals with a 30 cm diameter (Figure 2).

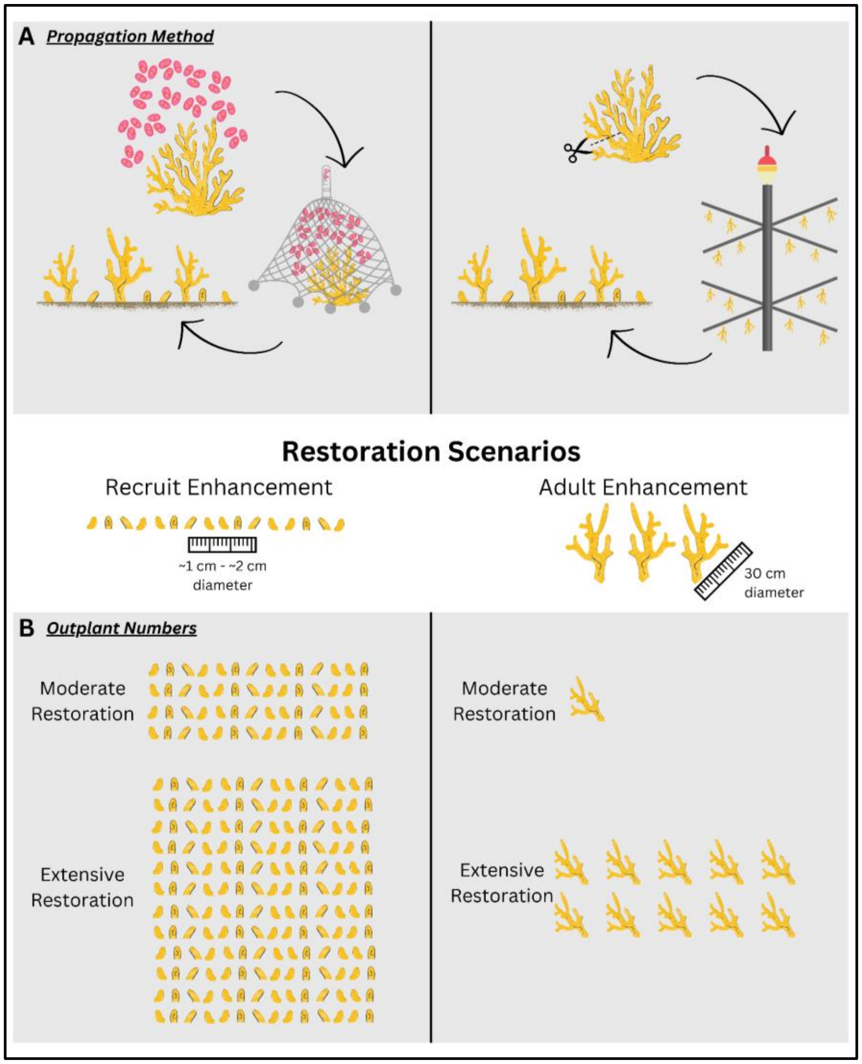

Figure 2. **Restoration Scenarios.** A graphical representation of each restoration scenario - (A) methods of propagation to generate different sized outplants, (B) the outplant quantity and coral size for each scenario.

Scenario 1 - Recruit Enhancement

Moderate Restoration

Recruit sized corals can be propagated from sexual propagation or asexual fragmentation. To determine a realistic number of recruits to outplant annually, sexual propagation efforts served as a baseline. Different restoration efforts collected spawn from an average of 30 adult colonies (either ex-situ or in-situ [colonies brought to a lab facility]) and resulted in anywhere from ~42,500 to 400,000, to over a million larvae (Cameron and Harrison, 2020; dela Cruz and

Harrison, 2017; Harrison et al., 2021). Of these collected larvae, a range of ~1000 to ~7000 settled spat were outplanted (dela Cruz and Harrison, 2017; Cameron and Harrison, 2020; Harrison et al., 2021). Yet, space is limited in restoration areas and a realistic number was selected for min/max recruit generation on an annual basis at an island scale based on the literature above. The number of outplanted recruits ranged from ~32 recruits per m^2 to ~220 recruits per m^2. This random vector of corals was added to the existing vector of corals each year in the model to simulate recruit enhancement.

Extensive Restoration

To appreciate the number of recruits and amount of outplanting necessary for recruit enhancement to add significant coverage, an extensive version of recruit enhancement was performed with three times the number of the recruits outplanted in the moderate restoration scenario. The number of outplanted recruits ranged from ~96 recruits per m^2 to ~660 recruits per m^2.

<u>*Scenario 2 - Adult Enhancement*</u>

Extensive Restoration

A local nursery in Guam served as a model for harvest methods and to quantity restoration through adult outplanting. The nursery has 22 trees with 144 coral fragments per tree. Not all trees host the same species, thus this model assumes two of those trees host the species of interest leaving 288 possible fragments for outplanting. Assuming fragments are harvested with a 10 cm diameter, it will take approximately three years for them to reach 30 cm diameter (following the growth model described above). This means a third of the corals are available for yearly outplant. In this model, these 96 corals will be distributed across the outer reef sites, thus 12 is the max number of fragments that can be introduced to any given site. As all corals might not be available each year either due to loss or slow growth, the model simulates an outplant of 10 corals per 4 m^2, or 2.5 corals/m^2, each year at a fixed size of 30 cm diameter. Each year, 10 colonies are added to the model to simulate restoration with large, adult corals.

Moderate Restoration

In order to better understand the outcomes and efforts associated with outplanting adults, an additional scenario was implemented, wherein a single 30 cm diameter colony was added annually (.25 corals/m^2). This scenario provided an opportunity to assess the impact of minimal restoration efforts.

Results

IPM Kernel

Non-Disturbance Growth Rates

The IPM kernel built with non-disturbance growth rates revealed a positive but low growth capacity of *Acropora* populations and that small to medium sized colonies (~2.5 - 5 cm^2 logarithmic or ~12 - 148 cm^2) have the highest probability for positive growth (Figure 3A). At approximately 5 cm^2 logarithmic (or 148 cm^2), *Acropora* populations began to experience negative growth indicative of both partial and post-settlement mortality ($\lambda = 0.66$). In support, the elasticity matrix identified this size range to be the most influential for growth (Figure 3B). Consequently, the transition between this size class and larger colonies was identified as the most sensitive for *Acropora* populations (Figure 3C). Despite only including non-disturbance years, the IPM yielded a slight decline in *Acropora* populations from their present state, or population shrinkage until the 2.5 - 5 cm^2 colony size becomes best represented. In sum, IPM with non-disturbance growth years forecasted that *Acropora* populations will persist on the ~4m^2

reef slopes being modeled but will undergo shrinkage and eventually be composed of medium sized colonies.

Net Growth Rates Including Disturbance Years

Different trends emerged from IPM when using net growth rates that included disturbance years. Growth rates were mainly negative indicating colony shrinkage with kernel hotspots residing under the 1:1 slope (Figure 3D). Once a colony exceeded ~3 cm^2 logarithmic (~20 cm^2), partial and post-settlement mortality began to occur and the overall population thus experienced shrinkage (Figure 3D). Elasticity and sensitivity matrices differed in their values but were similar in nature identifying the critical point where the full kernel hotspot began to fall below the 1:1 slope line as the most influential to *Acropora* growth rates and transitions (Figure 3 E and F, respectively) (~2.5 cm^2 logarithmic or ~12 cm^2). The disturbance IPM calculated a lower population growth rate of $\lambda = 0.15$, suggesting that *Acropora* would persist at low levels on the modeled reef slope habitats, but become significantly reduced in size if the disturbance regimes CNMI experienced over the past 15 years are indicative of the future.

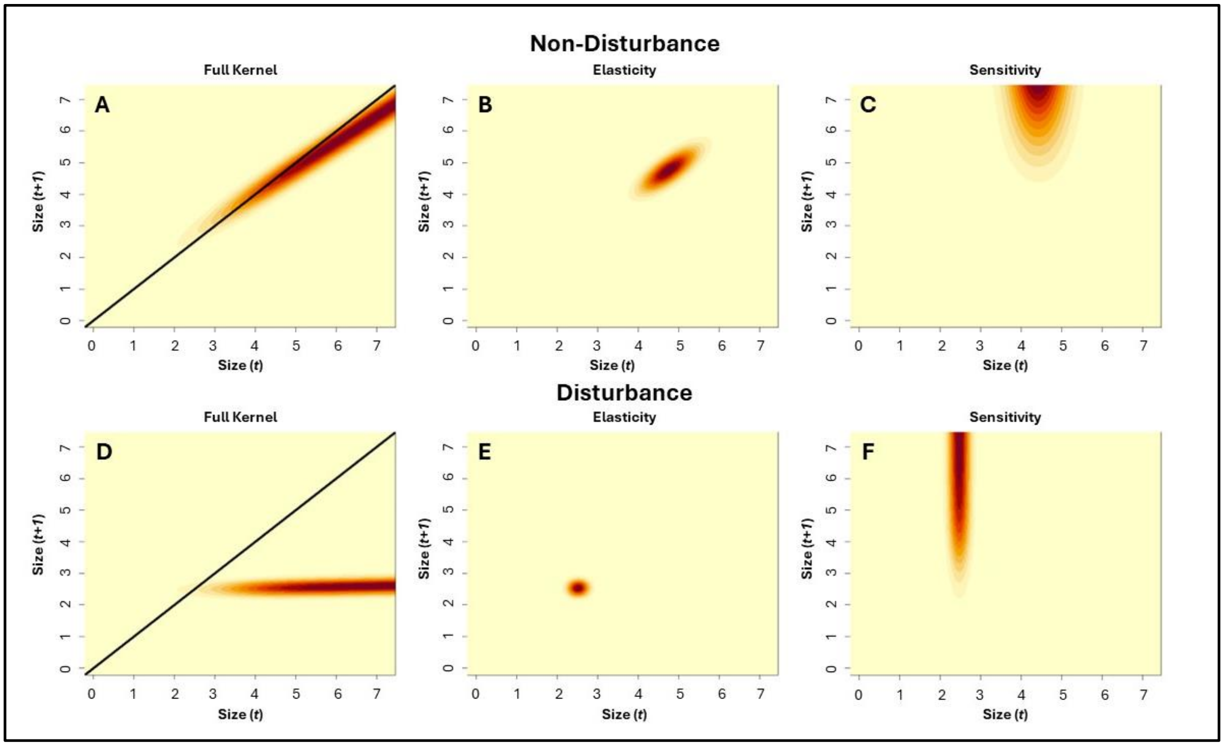

Figure 3. Integral Projection Model Kernels. Integral projection model outputs in a non-disturbance year (A-C) and a disturbance year (D-F). Panels A and D depict the entire IPM kernel. Warmer colors represent a higher probability of a size transition. The solid line is a 1:1 slope depicting no change in size between years. Panels B and E depict the IPM's elasticities. Panels C and F represent the IPM's sensitivities.

Discrete Model - Projection and Calibration

The discrete model was seeded with an initial vector representing the size distribution of corals recorded in Saipan in 2007 and 2008 – following a major COTS disturbance and thus simulating the recovery phase dynamics in the model. The 100 simulations of the discrete model revealed an initial increase in *Acropora* coverage with a peak between timestep 7 and 10 (~7%), followed by a decline and stabilization to ~3% cover (Figure 4A). The model data corresponded with long-term observations during this same time period that also revealed an initial increase with a peak around 2015 (i.e., timestep 8, ~4.5%) then a decline to ~1% following a major heat-stress event (Figure 4B). Observed data following the heat-stress event were not available to draw correspondence with the latter part of the discrete model, however, there was still a significant overall correlation between annual growth rates of the model versus observations (Pearsons r =

0.69). In addition to the overall correlation of annual growth rates, the effect size associated with coral cover comparisons at year 5 revealed non-significant differences (Figure 8). Further, comparisons of size-class distributions at timestep 5 revealed non-significant differences in the size structure of *Acropora* assemblages observed versus modeled based upon overlapping density distributions (Figure 7). In sum, three influential lines of evidence demonstrated the similarity between the discrete model simulations and the observed data regarding annual growth rates, coral cover comparisons, and size-structure comparisons. This supported the use of the discrete model for forecasting differing restoration scenarios.

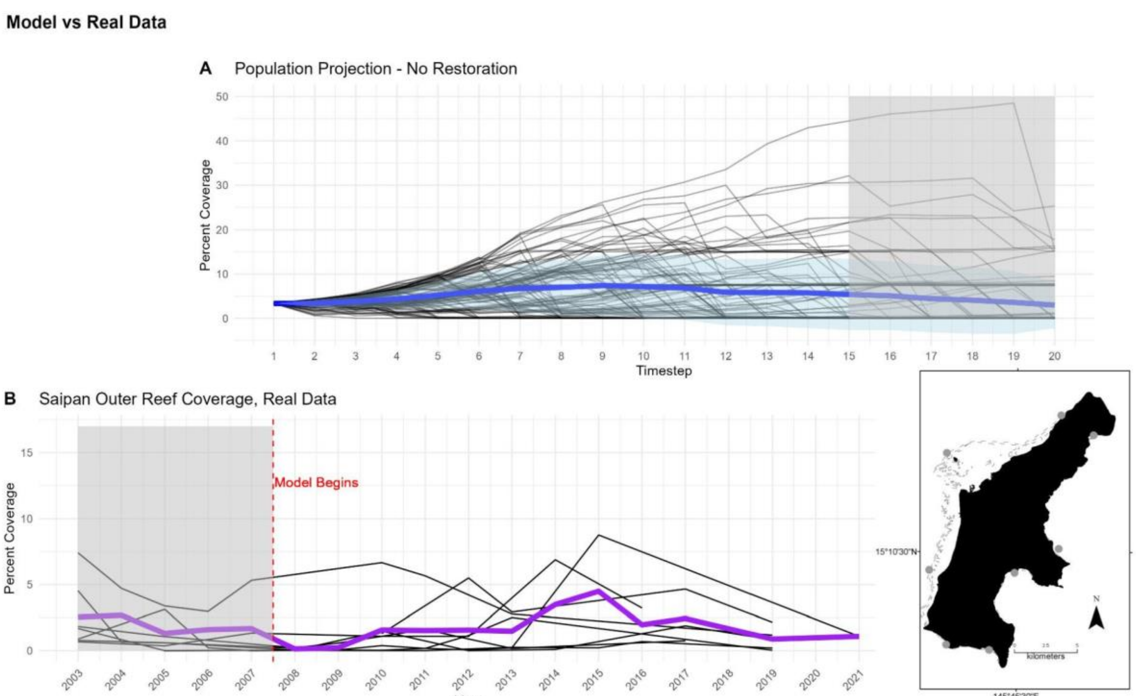

Figure 4. Model Projection vs Real Data. Figure A displays 100 simulations of a 20-year projection from the discrete IPM model. The purple line represents the average of the 100 simulations. Figure B illustrates plots of all the outer reef coverage values in Saipan from 2003 to 2021. The purple line represents the average coverage across all sites. The model begins between 2007 and 2008 of the real Saipan coverage. Figure C shows a map of Saipan and the eight outer reef locations.

Restoration Scenarios

Moderate Recruit Enhancement

By introducing anywhere between 31 recruits/m^2 to 219 recruits/m^2, there was an overall increase in average coverage as compared to the projection with no restoration (Figure 5A, 5.21% to 6.14% average cover at timestep 5, and 3% to 5.51% average cover at timestep 20). A correlation test revealed significant and strong positive correlation between the average coverage projection of no restoration and moderate recruit restoration (p-value = 7.568e-09, cor = 0.92). The correlation coefficient is close to 1 indicating a nearly perfect linear relationship. An ANOVA with post-hoc test was conducted to compare the percent coverage between the no restoration scenario and moderate recruit enhancement at year 5 and year 20 (Figure 8). However, statistical analysis revealed no significant difference in coverage between the no restoration model and recruit enhancement model for either year. This suggests only minimal increases in percent coverage compared to the base population coverage over the 20-year period, and that *Acropora* populations were close to their equilibrium in terms of coverage and size structure by year 5 of annual restoration efforts. In addition to the average coverage, the size distribution shifts to smaller sizes as compared to the no restoration model (Figure 7) further explaining the coverage trajectory. Overall, there is no significant increase in coverage through moderate recruit enhancement as compared to no restoration.

Extensive Recruit Enhancement

To understand just how much restoration effort would be required to have an impact, an extensive scenario introduced three times the number of recruits (93 recruits/m^2 to 657 recruits/m^2). Unlike the moderate restoration scenario, the average cover for the extensive scenario begins to separate from the population model with no restoration (Figure 5B, 5.21% to

6.61% average cover at timestep 5, and 3% to 9.85% average cover at timestep 20). While there is a visible increase in the percent cover line, the values were statistically similar with an average cover increase of ~7% that did not exceed the estimates of variability associated with no restoration. A correlation test reveals a significant and moderately strong positive correlation between the average cover projections (p-value = 0.02, cor = 0.53). The correlation coefficient is close to .53, indicating a partial linear relationship. Similar to the moderate recruit enhancement, an ANOVA with post-hoc test revealed no significant difference in coverage between the no restoration model and extensive recruit enhancement model for either year (Figure 8) and the size distribution shifts to smaller sizes as compared to the no restoration model (Figure 7). While there is a larger increase in average coverage as compared to the moderation recruit enhancement scenario, limited gains in cover existed in comparison to no restoration despite extensive recruit enhancement.

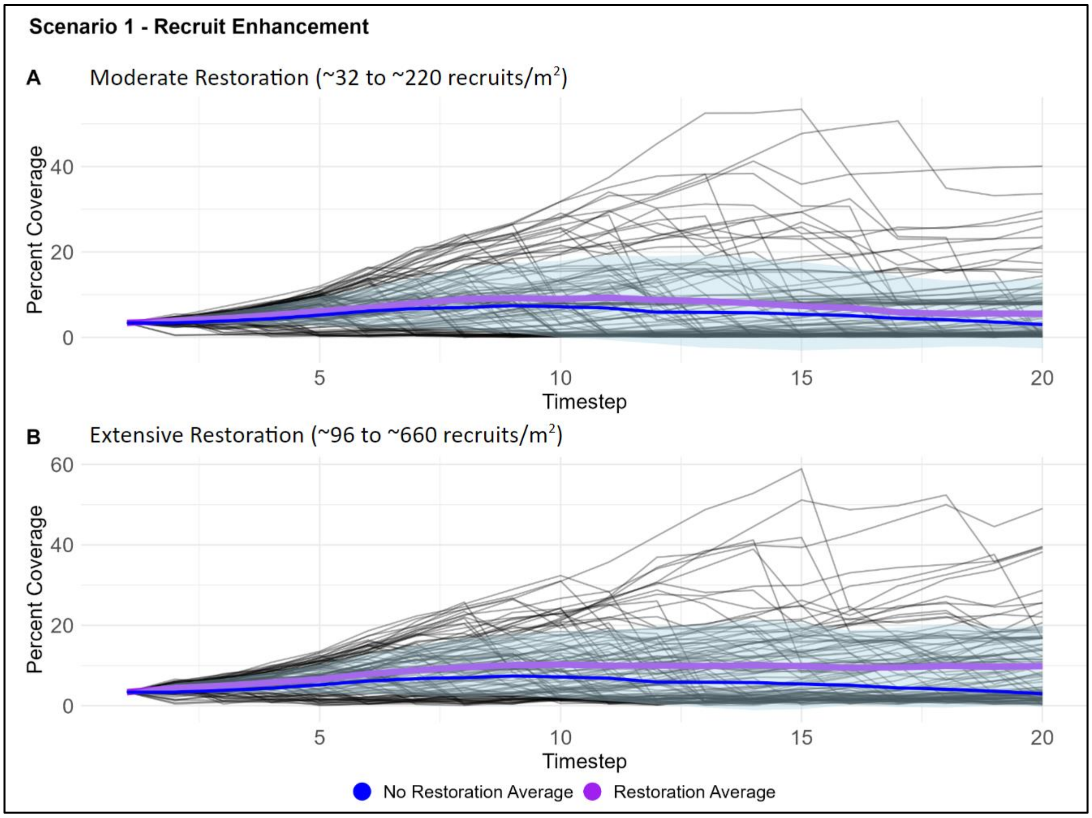

Figure 5. Recruit Enhancement Coverage. Recruit enhancement represents restoration by adding high quantities of small corals. The blue line represents the mean coverage from the population model demonstrating coverage when no restoration takes place. These projections represent 100 simulations of a 20-year projection. Panel A shows a realistic enhancement adding anywhere from 32 to 230 recruits per meter squared. The recruit enhancement average does not increase coverage when compared to the no restoration model. Panel B illustrates an unrealistic enhancement that adds 3 times the number of recruits.

Moderate Adult Enhancement

To understand what effect a minimal restoration effort of larger colonies would achieve, one coral of 30 cm diameter was introduced each year to the model (.25 corals/m^2). Compared to the no-restoration model, there was a significant increase in coverage (Figure 6A, 5.21% to 26% average cover at timestep 5, and 3% to 50.6% average cover at timestep 20). A correlation comparing the projection of adding 1 coral each year to the no restoration projection reveals an insignificant positive correlation (p-value = 0.08, cor = 0.39). An ANOVA with post-hoc test revealed a significant increase in coverage as compared to the no restoration model in year 5 and 20 (Figure 8), increasing in timestep 20, indicating the long-term benefits of intensive adult enhancement. From year 5 to 20, there is a shift in the size distribution from that similar to the no restoration model to larger than the no restoration model (Figure 7) further explaining the significant increase in coverage.

Extensive Adult Enhancement

By introducing ten corals of 30 cm diameter each year to the model (2.5 corals/m^2), there was a notable increase in coverage as compared to the no restoration model (Figure 6B, 5.21% to 160% average cover at timestep 5, and 3% to 389% average cover at timestep 20). This was accompanied by high variability in the model where all simulations exceeded 100% coverage with an unrealistic mean of ~400% cover because the model had no upper boundary. A correlation test revealed an insignificant positive correlation between the no restoration model projection and the projection of adding 10 adult corals to the reef (p-value = 0.33, cor = 0.23). An ANOVA with post-hoc test revealed a similar trend as the moderate adult enhancement with a significant increase in coverage in year 5 and 20 (Figure 8). Examining the size distribution, there is a shift in the size distribution from that similar to the no restoration model to larger than the no restoration model from year 5 to 20 as seen in the moderate adult enhancement model (Figure 7).

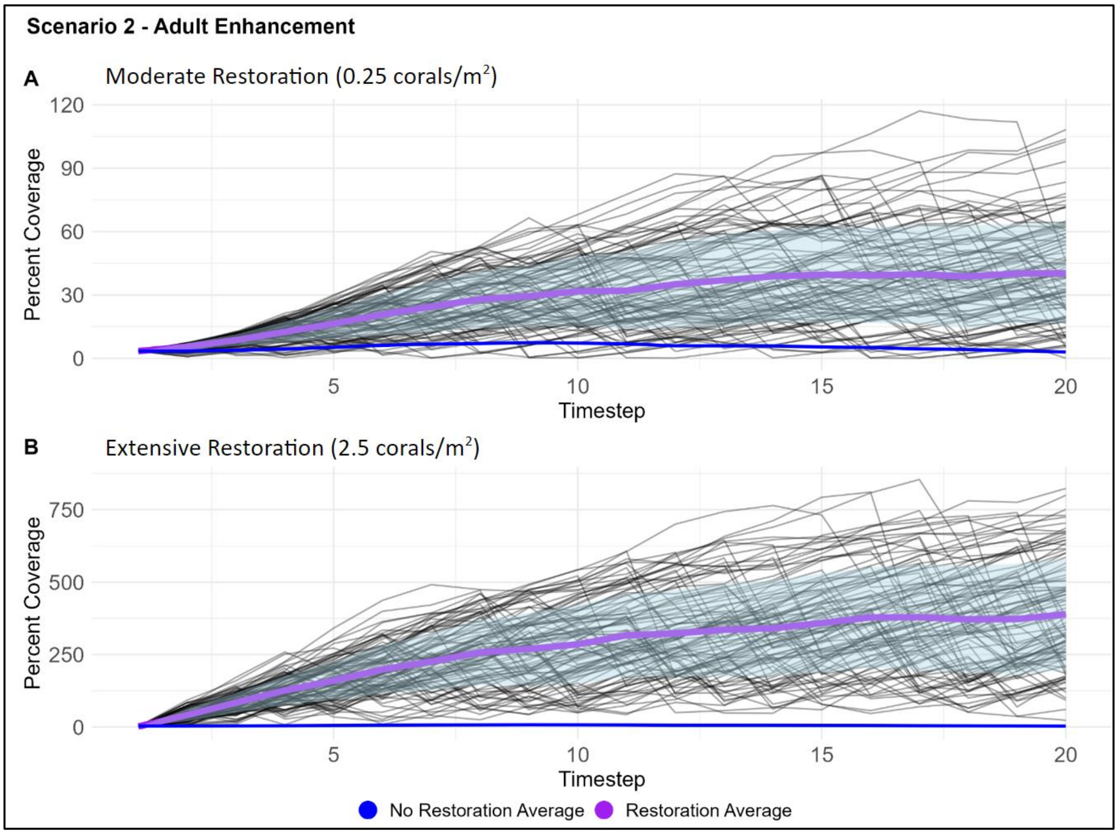

Figure 6. Adult Enhancement Coverage. Adult enhancement represents restoration through the outplant of adult corals. The blue line represents the mean coverage from the population model demonstrating coverage when no restoration takes place. These projections represent 100 simulations of a 20-year projection; the purple line represents the average coverage of each scenario. Panel A represents adding ten 30 cm diameter corals to the reef each year. Panel B represents outplanting one 30 cm diameter coral to the reef each year.

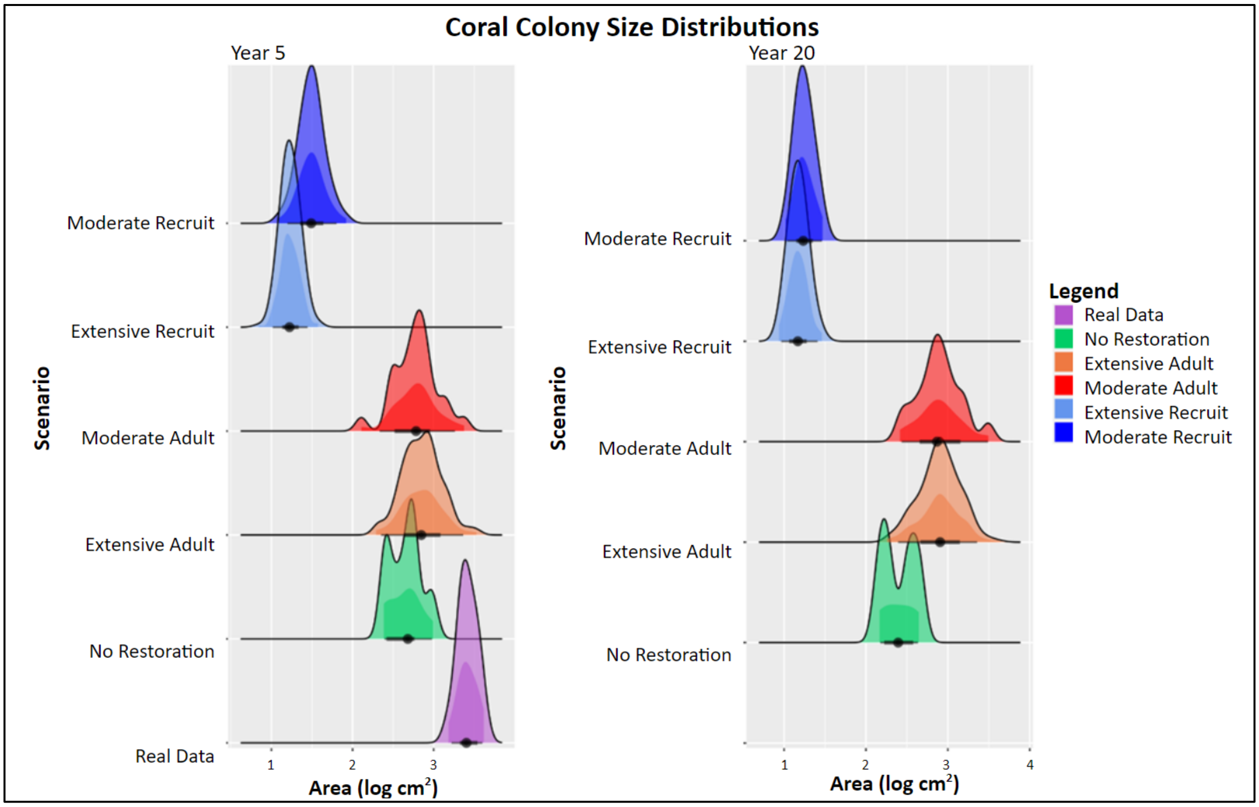

Figure 7. Size Distributions Comparison. Comparison of each scenario's size distribution at year 5 and 20. The dot on the x axis of each represents the mean and the lines represent the median and 95% confidence interval.

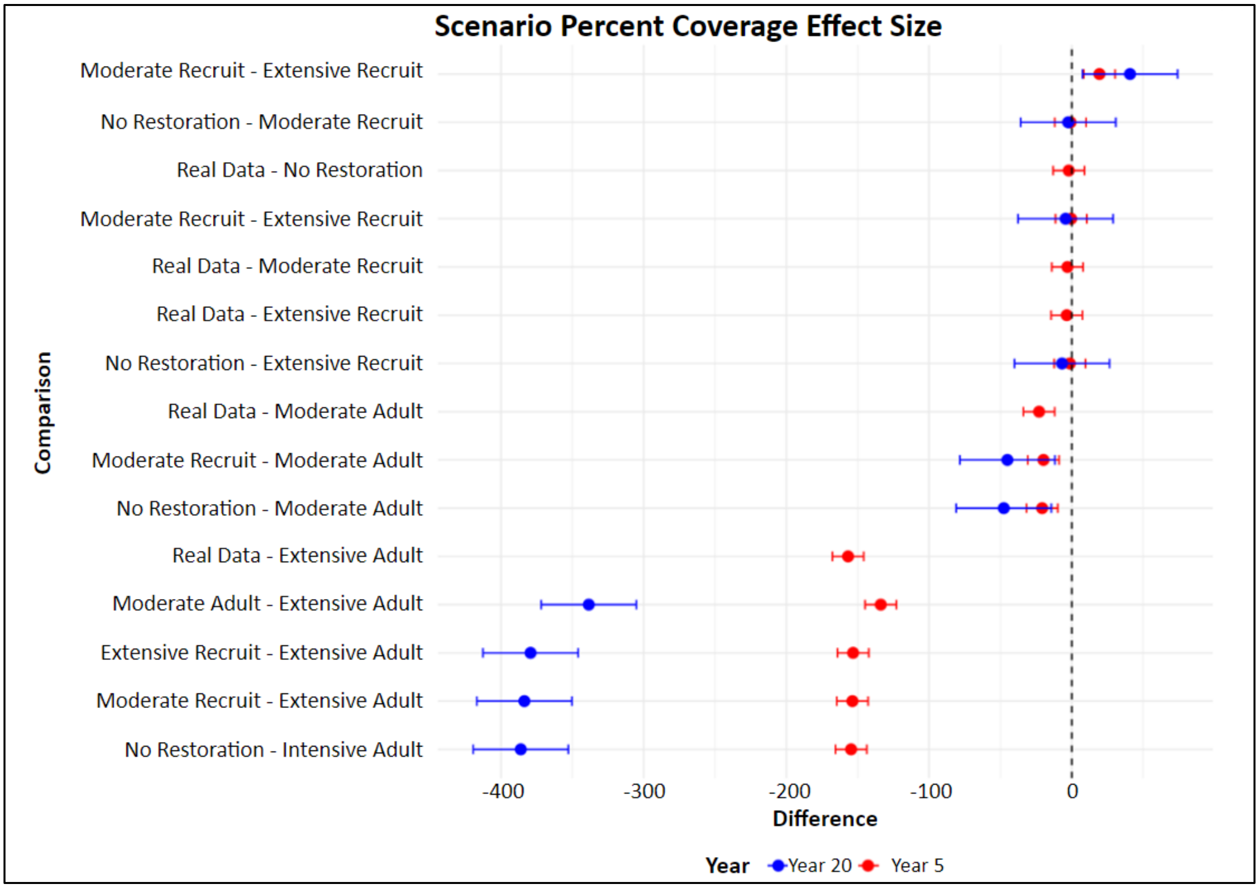

Figure 8. Statistical Effect Size Comparison. Compares the result of an ANOVA Tukey Test effect size examining percent coverage at timestep 5 and 20. The red dots represent year 5 and the blue dots represent year 20.

Discussion

Digitate and corymbose *Acropora* populations have historically been dominant on outer reef slopes across Pacific Islands such as Saipan, CNMI, but have been declining in recent years due to combined chronic and acute stressors. The modeling environments were scaled to reflect the realities of a typical island and used net growth rates associated with both disturbance and non-disturbance years to evaluate restoration. The IPM highlighted the critical sizes of *Acropora* populations beyond which significant mortality occurred, thus setting the stage for restoration objectives. Two restoration scenarios were selected based upon these findings with outplanted coral sizes below and above this threshold defined by the IPM.

In the case of Saipan, adult enhancement emerged as the most effective approach to restoration. Unlike the other kernels described in a past coral study that used with brooding *Porites* corals (Shlesinger and van Woesik, 2021), neither the disturbance nor non-disturbance kernel exhibited a recruitment and reproduction "hotspot", suggesting that recruitment limitation was not the primary driver of Acropora populations on the 8m reef slopes. This key finding may differ depending on the exact reef habitat observed (lagoon, reef crest, reef slope), but similar findings were observed in Saipan, CNMI by Houk et al. (2010) who identified post-settlement mortality as the strongest driver of reef slope population dynamics in Saipan. Modeling of recruit enhancement under extremely high densities did improve the coverage but did not address the shrinking size class distribution that is impacting *Acropora* populations under current stressor regimes. Such findings underscore the intricate and complex dynamics inherent in population ecology and their interplay with varying restoration approaches. In contrast, adult enhancement methodologies showed a clear increase in reef coverage; as evidenced when adding 10 corals annually (2.5 corals/m^2), greater than 100% coverage and maximum average coverage of 389% after 20 years were achieved – the equivalent of 15.56 m^2 (Figure 9).

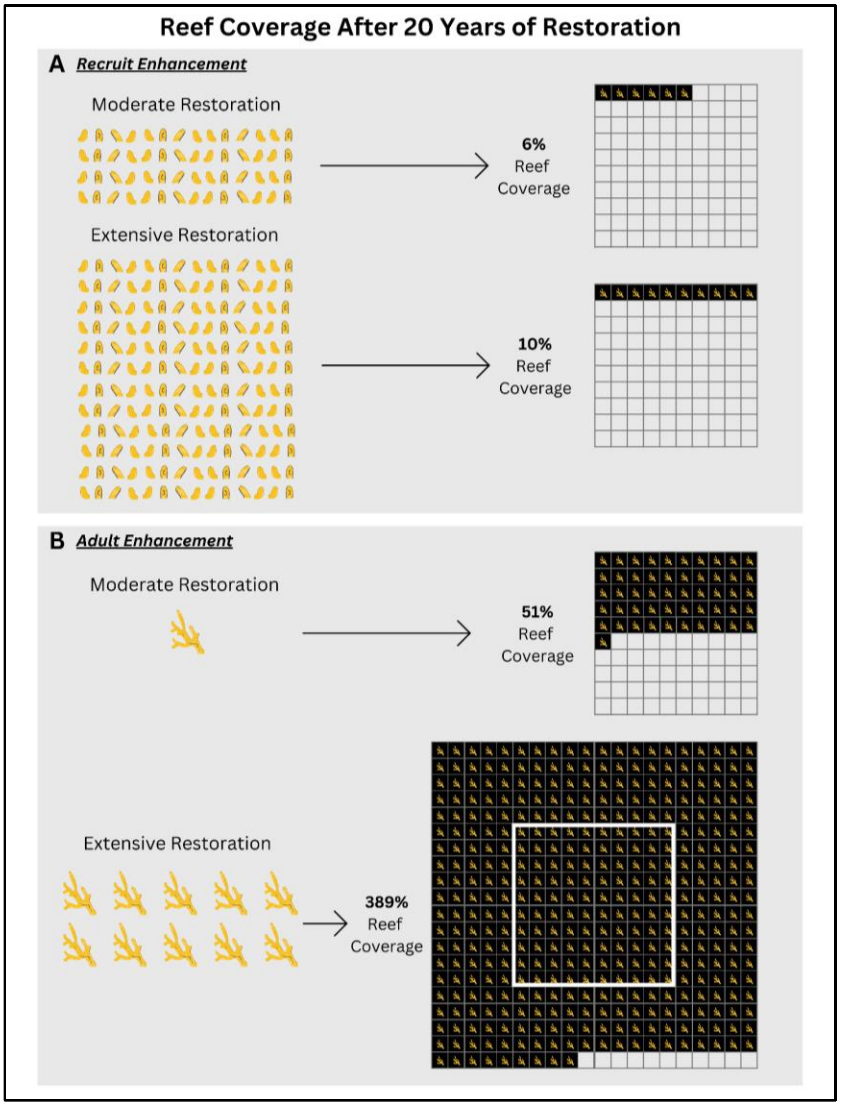

Figure 9. Scenario Summary. A graphical representation of each restoration scenario's resulting coverage after 20 years. The coverage is scaled to 4 m^2 of reef - equivalent to the total reef surveyed in the transects. (A) Displays the coverage for recruit enhancement. (B) Displays the coverage for adult enhancement.

While Saipan is a small island in the Western Pacific with unique population dynamics and disturbances, it is not dissimilar from many reef communities harboring other coral species. In the Great Barrier Reef, studies have revealed a naturally occurring high mortality rate among newly settled broadcast spawning juvenile corals (67-99%; Babcock, 1985; Babcock & Mundy, 1996). van Woesik et al. (1999) found that physically harsh environments are a key mechanism in shaping communities through differing mortality rates. These harsh environments can be created through local stressors including runoff and sedimentation or more global stressors including warming oceans or acidification. In the case of *Acroporas* on nearshore fringing reefs in Panama, Curacao, and Bonaire, post settlement mortality (due to sedimentation, predation, and space competition with r-selected species (small, fast-growing, and rapid sexual maturation) like crustose coralline algae, ascidians, and barnacles), is the primary force structuring reef dynamics (Bak and Engel, 1979; Birkeland, 1977). Coral demographic studies conducted across degraded reefs globally have shown current levels of recruitment are insufficient to compensate for declines in adult survivorship required for population survival (Bak and Meesters, 1999; Chui and Ang Jr, 2017; Guerrini et al., 2020; Hughes and Tanner, 2000). As highlighted in Chui et al. (2017) this "recruitment failure" can also originate from low settlement attributed to reduced survival in the planktonic larval stage due to reduced salinity from increased precipitation or runoff, spatial difficulties with long planktonic stage larval not being retained in the origin reef or limited larval supply due to isolation. This isolation is caused by both local and global stressors leading to coral decline. Synthesis of data from 1974 to 2012 across the tropics revealed coral recruitment has been reduced by over 80% in the tropics and increased in the subtropics indicating a poleward shift in recruitment due to climate change (Price et al., 2019). A study at Palmyra Atoll from 2013 to 2017 examined survival patterns of juvenile corals and determined only 40.8% of the juveniles survived (Sarribouette et al., 2022). Sarribouette notes that comparisons across juvenile survival studies should be made with caution as each study employs different methodologies over varying timescales and did not take into account episodic or severe disturbances and stressors. As evidenced above, global stressors are augmenting and disrupting natural settlement and post settlement processes and survival. While Saipan served as a case study for this modeling approach to understanding restoration, the findings can be applied to reefs globally.

Coverage, however, is not the only factor to consider. Different sized fragments can be generated from either asexual fragmentation or sexual propagation. Fragmentation is a method in which a parent colony is broken into smaller, separate parts (Plucer-Rosario & Randall, 1987; Vaughan, 2021) and fragments are subsequently outplanted. A systematic review of coral restoration efforts found coral gardening – cultivating coral growth in nurseries – to be a sustainable method of restoration due to (1) its successful survival rates (66%) and (2) mitigation of the need to harvest naturally occurring coral fragments if the nursery step is skipped (Boström-Einarsson et al., 2020). Despite the success of the fragmentation method, there are concerns this approach could result in genetic homogeneity due to clonality, leading to disease vulnerability and limited ability to adapt to stressors at the population level (Vaughan, 2021). Sexual propagation as a method of coral restoration can mitigate some of the drawbacks introduced through fragmentation; however, there are also disadvantages. Advantages include (1) greatly increasing genetic diversity of outplanted corals in comparison to fragmented corals, and (2) eliminating physical damage to source reefs (Guest et al., 2014). Because corals are notably fecund, harnessing their sexual reproduction has the potential to capture millions of propagules (Guest et al., 2014), facilitate a robust restoration effort, and promote resilience through increased diversity (Boch & Morse, 2012). Disadvantages include spawning collection which often requires ex-situ lab facilities that increase overall research costs (Epstein et al., 2001) and significantly increase labor to collect, maintain, settle, and outplant the sexually propagated recruits (Guest et al., 2014). Coral colonies are often geographically separated, preventing successful fertilization in nature (Boström-Einarsson et al., 2020) and making collection difficult. While larvae collection can result in large numbers of recruits that are easier to transplant and outplant in large numbers as compared to larger colonies, the combination of high mortality rates, labor intensity, and laboratory access makes this method of collection and restoration extremely challenging. There is significant work being done examining coral genetics and trying to find thermally resistant colonies and use them in restoration called assisted evolution. However, while assisted evolution has the potential to improve long-term coral cover, it does not have the capacity to prevent severe declines due to climate change (DeFilippo et al., 2022).

Reef restoration practitioners face many dilemmas when choosing which methods to pursue and deciding on the location and scale of outplanting. To put this in perspective, in order to restore all the outer reef slopes in Saipan (4.5 km^2) to 50% coverage, a restoration program would have to outplant approximately 1,125,000 30-cm diameter corals (~700 cm^2) annually for 20 years. Consideration of time, resources, funding, population dynamics, and pros and cons of different propagation methods is critical to achieving the desired restoration outcome. Coral restoration is still in its nascent stage both in the scientific and commercial fields. Spatially, the majority of projects are conducted on a small scale. In their review, Boström-Einarsson et al. (2020) found the median size of restored reefs to be $100m^2$. While sexual propagation has the potential to scale up restoration given the large amounts of recruits generated, this method is still limited given the global dynamic of post settlement and recruit mortality on reefs. Restoration practitioners and scientists have yet to develop effective, economically replicable, and sustainable methods at large scale due to the above cited difficulties associated with restoration. Advancements on the technological front must be recognized, analyzed, and married with ecological theory to scale up the efficacy of restoration globally.

Taking this first step of creating a framework for restoration decision-making has the potential to significantly increase successful outcomes by enabling practitioners to identify and better understand the population dynamics of target sites. Being able to weigh potential outcomes will contribute directly to project planning and cost-benefit analysis. Project budgeting is a common and significant challenge for restoration as funds are almost always limited; this invariably leads to a lack of long-term monitoring as funds are often redirected (Saunders et al. 2022). The ability to better forecast which method(s) offer the most cost-effective and strategic path forward will empower practitioners to effectively analyze, develop, advocate for, and execute coral restoration projects.

This model is, to our knowledge, one of the first attempts to model coral restoration efforts using a size-based model. The IPM unveiled the underlying population dynamics influencing Saipan’s outer reefs; specifically, post settlement mortality prevailed as the prominent force. This explained the success of adult enhancement as a restoration approach. Coral cover and size distributions benefitted over the course of 20 years from outplanting 30 cm diameter coral colonies.

Application of IPM-driven discrete modeling represents a ground-breaking step forward in conceptualizing coral restoration efforts. By disentangling ecological dynamics at a population level, this approach lays a foundational framework for more intricate models with additional variables. Combined with future interdisciplinary efforts, this novel approach has the potential to facilitate and enhance holistic restoration approaches and decision-making – a pathway to a restoration renaissance. This model found outplanting fewer, larger corals and investing the time to produce larger colonies represents the most promising method in the face of climate change. Innovation and future technological approaches that produce millions of recruits have the potential to enhance restoration. This is a “plug and chug” model and can be applied to any species, any reef, any disturbance, in any part of the world and examine different size regime restoration efforts. Expensive and time intensive, restoration is in its nascent stage, but we can now apply lessons learned and population dynamics to save time, money, and maximize restoration success.

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