Mathematical Model and Analysis of the Effects of Overfishing on Coral Reef Ecosystems
Coral Reefsearchers

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1   Introduction

Coral reefs play a crucial role in the marine's ecosystem as it serves a purpose for an abundance of marine life. Additionally, healthy coral reefs benefit the economy as it provides jobs and businesses through tourism and local fisheries. Unfortunately, in the recent years the health of coral reefs have been declining due to several factors. According to a 2008 world coral reef status report, it predicts that 15% of all coral are in danger of disappearing within 10-20 years, and 20% within 20-40 years [9].

With climate change rates increasing, one of the prevalent factors affecting coral reefs is rising sea temperatures, which leads to mass bleaching of corals. Other destructive environmental factors include ocean acidification, nutrient flow from run-off [9]. Another factor that contributes to the decline of healthy coral reefs are due to human activities, such as exploitative fishing practices or pollution [7].

Because a handful of coral species are considered to be threatened, efforts in measuring the resiliency factors of a coral reef has been of interest to many. In one study, ecological factors were studied and scored in which resistance, recovery, and resilience were taken into account. It claimed the top three ecological factors that contribute a coral's resiliency is its species type, temperature variability, and nutrients for pollution run-off [10].

The objective of this paper is to analyze how Guam's reef ecosystem will change over the coming decades, focusing on the impact of overfishing of parrotfish. By setting up a compartment model and subsequent system of differential equations, we are able to model the dynamics of the ecosystem in response to different parameter and compartment values. This will allow us to analyze and predict the effect of overfishing on Guam's coral reef ecosystem. In addition, our analysis will include the application of education game theory in order to quantify the human factor in overfishing.

2 Mathematical Model

2.1 Coral Reef Ecosystem Model
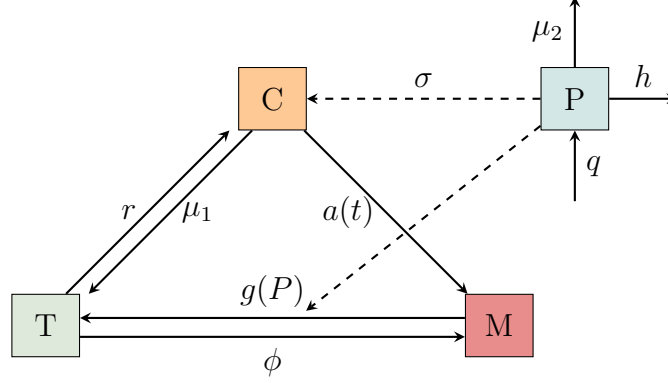
We assume that the ecosystem is (i) closed, (ii) consists of only corals, algal turfs, and macroalgae, and (iii) supports the maximum carrying capacity of parrotfish. We also assume that (iv) macroalage is the only predator of corals, that (v) corals recruit and overgrow algal turfs[7], that (vi) they are overgrown by macroalgae [7], and that (vii) macroalgae colonize dead coral by spreading vegetative over algal turfs [7]. Lastly, we assume that (vii) corals do not naturally die. Since corals have a natural life span of potentially thousands of years, we assume that they simply do not die naturally[1]. Rather, we still do take into consideration coral death by other means such as bleaching and disease.

2.2 Differential Equations

C, T, and M are proportions of coral, algal turf, and macroalgae cover on the ocean floor, respectively, and P is the population of the parrotfish that inhabit the coral reef ecosystem in proportion to the maximum carrying capacity. Since we assume that the ecosystem only consists corals, algal turfs, and macroalgae, we conclude that $C + T + M = 1$ such that they make up 100% of the ecosystem. Parrotfish are excluded from this dynamic as they do not require ocean floor surface area to survive. Rather, they exist in the water column above. As such, the coral reef dynamics are described as a system of nonlinear differential equations [2]:

$$\frac{dC}{dt} = rTC + \sigma PC - (a(t)M + \mu_1)C \tag{1}$$

$$\frac{dT}{dt} = \mu_1 C + \frac{g(P)M}{M + T} - T(rC + \phi M) \tag{2}$$

$$\frac{dM}{dt} = (a(t)C + \phi T)M - \frac{g(P)M}{M + T} \tag{3}$$

$$\frac{dP}{dt} = qP\left(1 - \frac{P}{\beta C}\right) - P(h + \mu_2) \tag{4}$$

2

where

$$g(P) = \frac{\omega P}{\beta}, a(t) = |\frac{a_0(9\sin{(\pi t)} + 1)}{10}|$$

and

$\frac{g(P)M}{M + T}$ is the proportion of grazing that affects macroalgae[2].

2.3 Parameter Values

In order to properly model our ecosystem, we analyzed various sources to compile parameters to use. Most of our sources are annual, or yearly, rates, and as our model is designed to use proportions, our parameters must also be values between 0 - 1. For example, our harvesting rate, h, is 0.14 per year, meaning 14% of the proportion of parrotfish are harvest per year. These are all our parameter variables, definitions, and values:

| Parameter	Description	Value	Units[8][7][2]
μ_1	natural death rate of coral reefs	0.15 [11]	$year^{-1}$
μ_2	natural death rate of parrotfish	0.22 [8]	$year^{-1}$
r	rate that coral recruit to overgrow algal turfs	0.5 [11]	$year^{-1}$
ϕ	rate that macroalgae spread vegetative over algal turfs	0.8[7]	$year^{-1}$
q	intrinsic growth rate for parrotfish	0.47 [8]	$year^{-1}$
h	harvesting rate for parrotfish	0.14 [8]	$year^{-1}$
σ	rate that parrot fish bite coral	0.01*	$bites * year^{-1}$
ω	maximum grazing intensity	1[2]	-
β	carrying capacity of parrotfish	1	-
a_0	control variable to simulate seasonal changes	0.99	-

Table 1: Model Parameters

*= estimated values
# = Guam specific parameters

2.4 Graphs

Utilizing Matlab, we are able to visualize our compartment model both by changing initial conditions and by changing parameter values, as shown below.
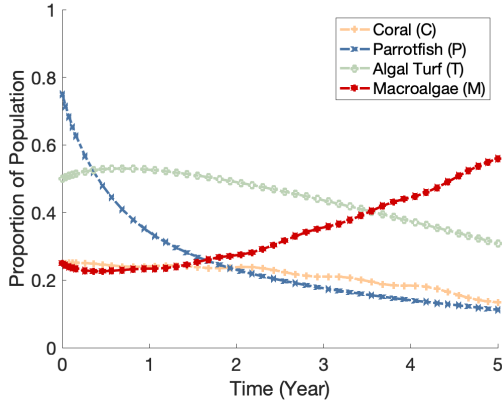
2.4.1 Initial Condition Variations

We were able to model the dynamics using our preliminary rates. This was achieved by changing the C, M, & T proportions. Below are the graphs that were were able to achieve:
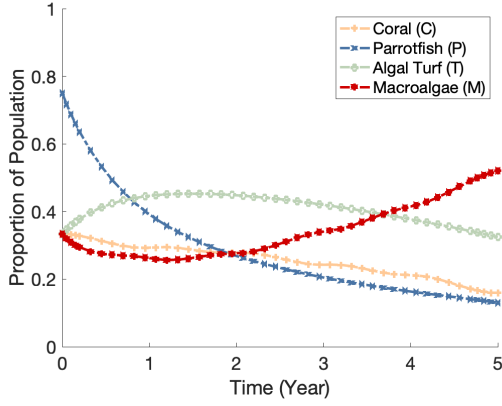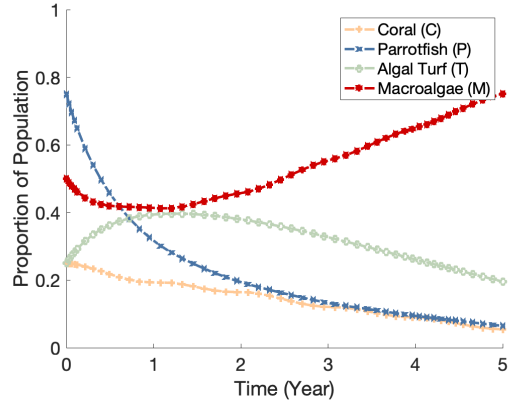
(a) IC: $C = T = M = \frac{1}{3}$, and $P = \frac{3}{4}$
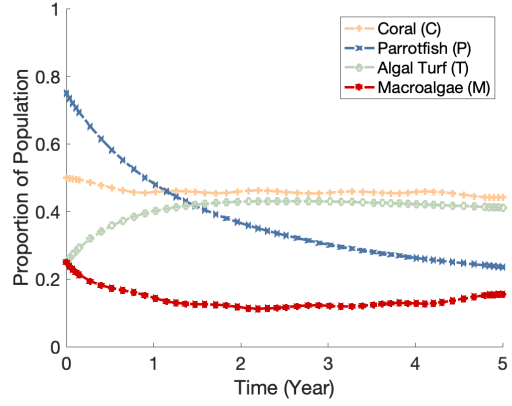
(b) IC: $C = \frac{1}{2}$, $T = M = \frac{1}{4}$, and $P = \frac{3}{4}$

(c) IC: $T = \frac{1}{2}$, $C = M = \frac{1}{4}$, and $P = \frac{3}{4}$

(d) IC: $M = \frac{1}{2}$, $C = T = \frac{1}{4}$, and $P = \frac{3}{4}$

Figure 1: Varied Initial Conditions (IC) using Parameter Values

As we can see in Figures 1.a, 1.b, 1.c, and 1.c, as the parrot fish population decreases, the macroalgae proportion increases. In addition, as the macroalgae proportion increases, the coral proportion decreases, and subsequently the algal turf proportion decreases as well.

2.4.2 Parameter Variation: a_0

Furthermore, we also analyzed the response of our model in response to changes in parameter values. The first of which we analyzed was with our seasonal simulation parameter: a_0.

(a) $a_0 = 0.02$

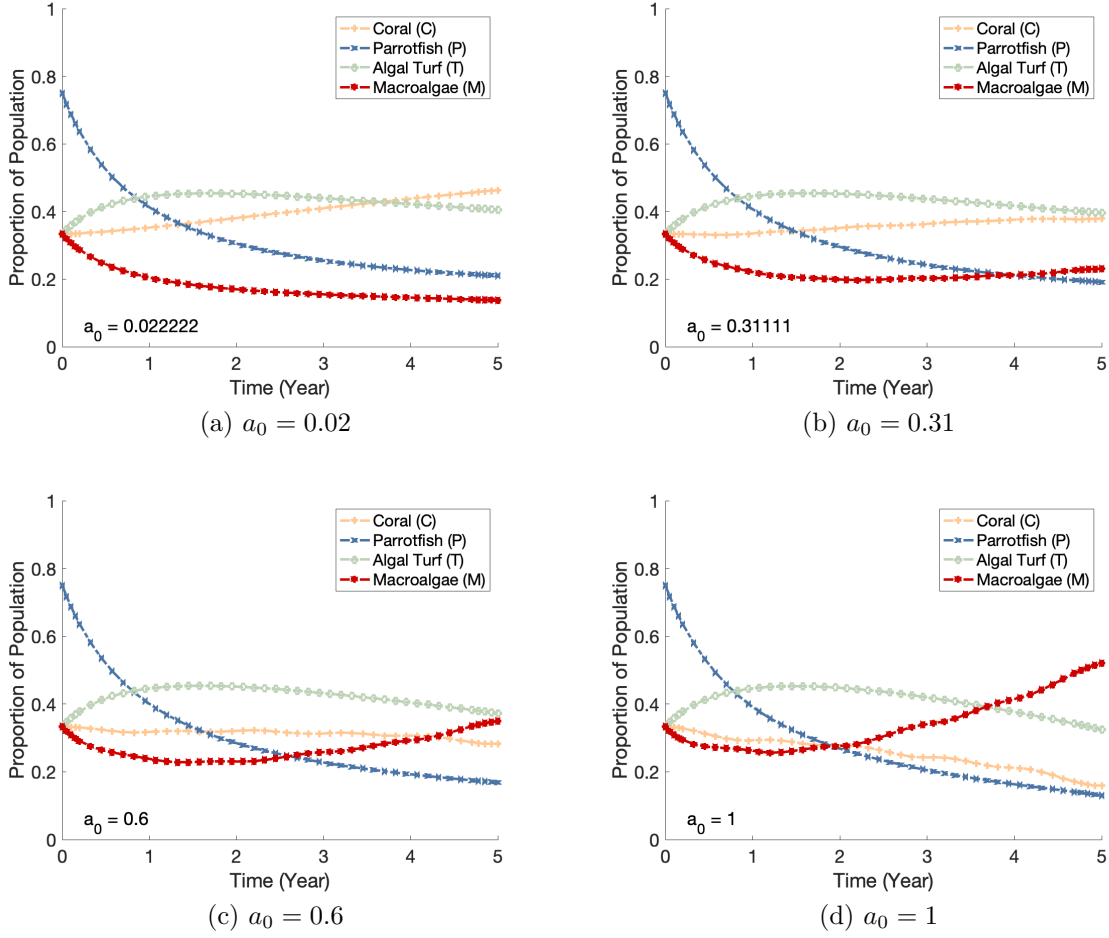(b) $a_0 = 0.31$

(c) $a_0 = 0.6$

(d) $a_0 = 1$

Figure 2: Various a_0 values with IC: $C = T = M = \frac{1}{3}$ & $P = \frac{3}{4}$

From Figures 2.a, 2.b, 2.c, and 2.d, we find that taking into consideration seasonal growth bursts of macroalgae does indeed have a significant effect on our model. As the control parameter, a_0, increases, the proportion of macroalgae also significantly increases.

2.4.3   Parameter Variation: h

Analysis of our harvesting rate, h, has shown us that the model dynamics is significantly influenced by the harvesting rate of parrotfish. Below are graphical visualizations of our ecosystem proportions at various harvesting rates:

(a) $h = 0.02$

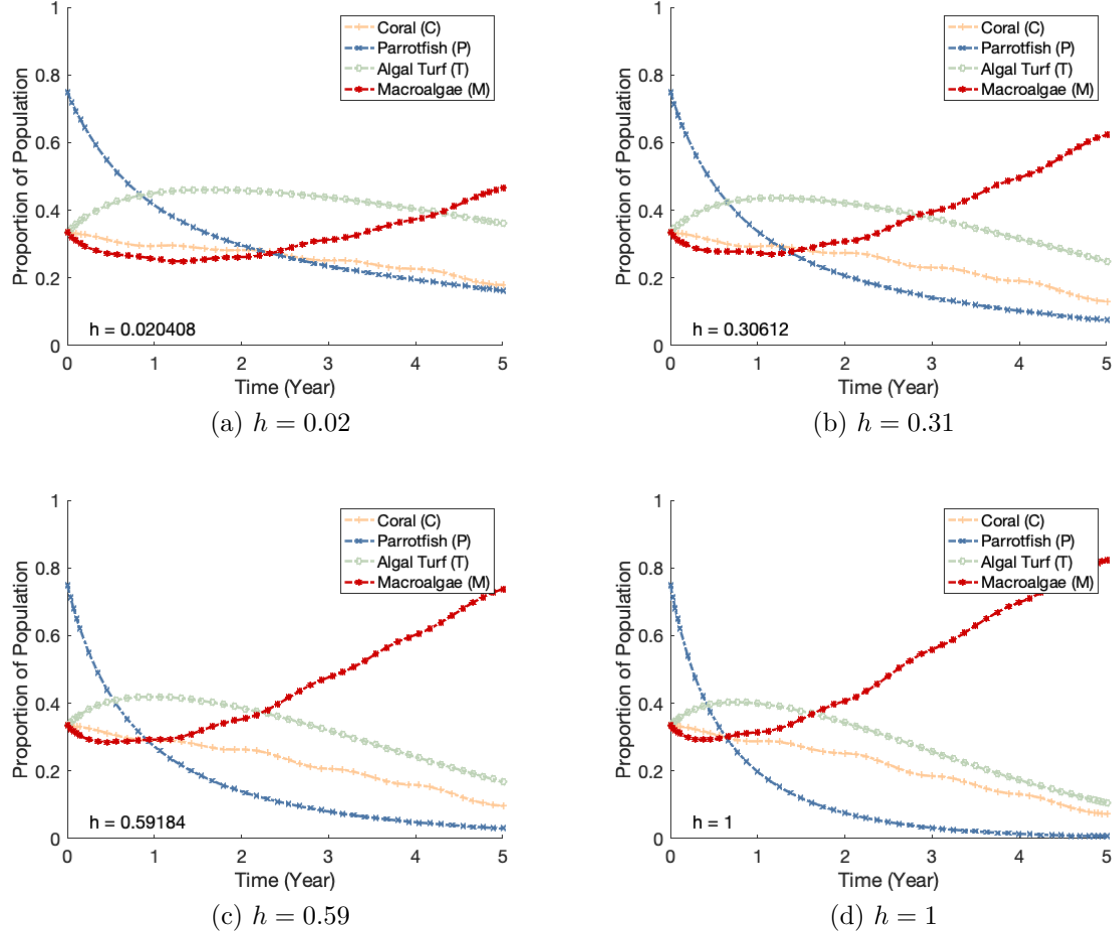(b) $h = 0.31$

(c) $h = 0.59$

(d) $h = 1$

Figure 3: Various h values with IC: $C = T = M = \frac{1}{3}$ & $P = \frac{3}{4}$

From Figures 3.a, 3.b, 3.c, and 3.d, we find that the h determines the state of the ecosystem, and as our harvesting rate increases, the ecosystem free-falls deeper into a morbidly macroalgae dominant ecosystem.

2.4.4 Parameter Variation: ϕ

Analysis of the rate at which macroalgae spread vegetative over algal turfs, ϕ, has shown us that the model dynamics suggest the parameter may have a larger impact than suggested:
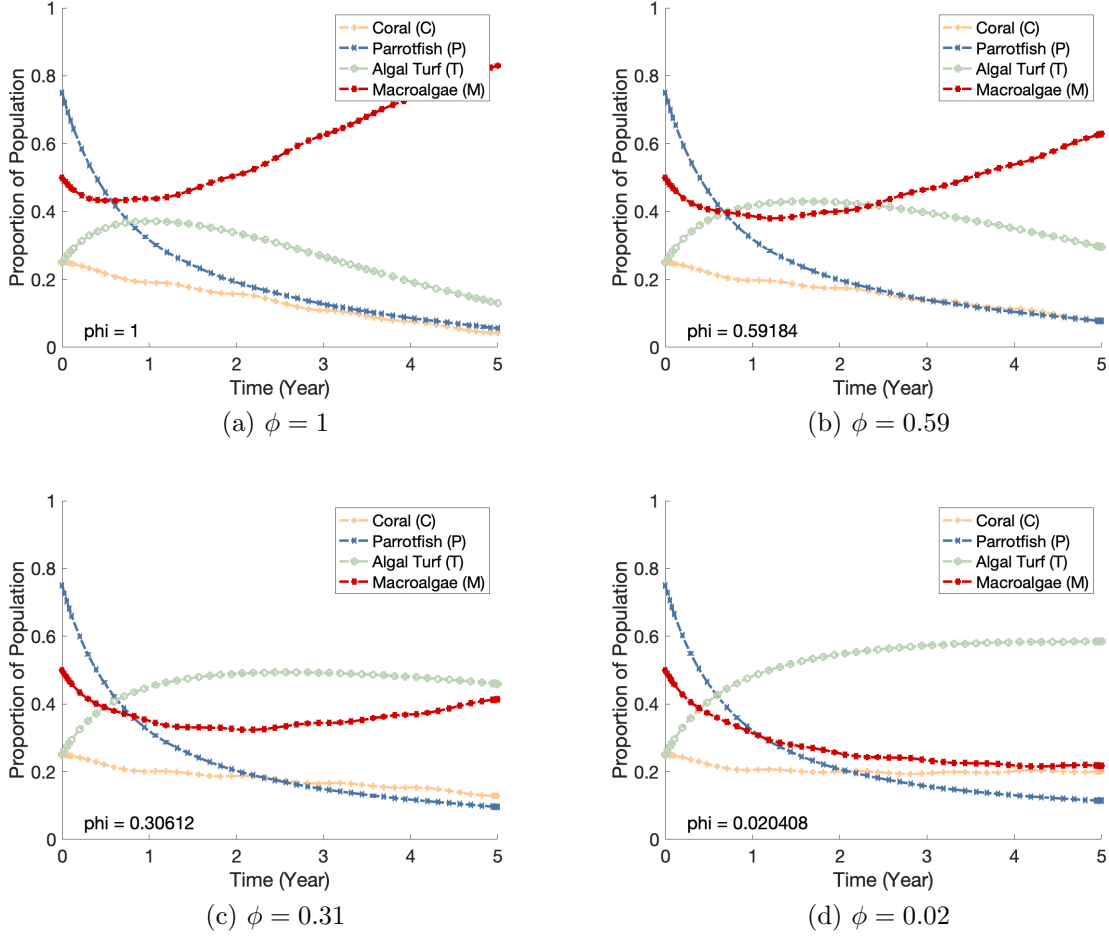
(a) $\phi = 1$ (b) $\phi = 0.59$

(c) $\phi = 0.31$ (d) $\phi = 0.02$

Figure 4: Various ϕ values with IC: $M = \frac{1}{2}$, $C = T = \frac{1}{4}$, & $P = \frac{3}{4}$

From Figures 4.a, 4.b, 4.c, and 4.d, we find that a decreasing ϕ results in an increased proportion of algal turfs, and subsequently will lead to an increased proportion of corals, as algal turfs are capable of recruiting corals. This parameter can be an excellent candidate to apply game theory in terms of control measures such as coastal and/or algal cleanups.

3   Equilibria Analysis

3.1   Disease-Free Equilibrium

The disease-free equilibrium, or DFE, is the point at which no disease is present in the system. Typically, this method is performed on disease modeling, however can be adapted to other types of modeling as well. In our model, we classify macroalgae (M) as our "disease" compartment, and since the system is disease free, we set $M^0 = 0$. Below is the result of our DFE calculations (detailed in Appendix A.1):

$$C^0 = 1 - \frac{\mu_1}{r}$$

$$T^0 = \frac{\mu_1}{r}$$

$$M^0 = 0$$

$$P^0 = -\frac{\beta(1 - \frac{\mu_1}{r})(h - \mu_2 - q)}{q}$$

Since our model was set-up so as $C + T + M = 1$ and since $M^0 = 0$, then we conclude that $C^0 + T^0 = 1$. Thus, our disease-free equilibrium is $(1 - \frac{\mu_1}{r}, -\frac{\beta(1 - \frac{\mu_1}{r})(h - \mu_2 - q)}{q}, 0, \frac{\mu_1}{r})$.

3.2 Endemic Equilibrium

The endemic equilibrium determines the point at which the disease will not spread nor will it fully eradicate. Essentially, it indicates when the disease is stabilized. In order to find the endemic equilibrium, we set each differential equal to 0 and solve for each variable. The equations are in terms of M (our disease compartment), as shown below (detailed in Appendix A.2):

$$C^* = 1 - \left(\frac{\mu_1 + a(t)M^*}{r} + M^* \right)$$

$$T^* = \frac{\mu_1 + a(t)M^*}{r}$$

$$M^* = \frac{\omega(\beta\left(1 - \left(\frac{\mu_1 + a(t)M^*}{r} + M^*\right)\right)\left(\frac{q - (h + \mu_2)}{q}\right))}{\beta(a(t)(1 - \left(\frac{\mu_1 + a(t)M^*}{r} + M^*\right)) + \phi\frac{\mu_1 + a(t)M^*}{r})} - \frac{\mu_1 + a(t)M^*}{r}$$

$$P^* = \beta\left(1 - \left(\frac{\mu_1 + a(t)M^*}{r} + M^* \right)\right)\left(\frac{q - (h + \mu_2)}{q} \right)$$

While not a disease model, the endemic equilibrium equations are significant in our research project as it is essential in order to perform game theory on our model.

3.3 Basic Reproduction Number: $\mathscr{R}_0$

The basic reproduction number, $\mathscr{R}_0$, is a metric used to describe the contagiousness or transmissibility of infectious agents[4]. In essence, this equation measures the number of secondary infections. Since our model is not disease-based, we conclude that our $\mathscr{R}_0$ symbolizes the rate at which macroalgae spreads after the initial macroalgae overgrowth. Our model recognizes macroalgae (M) as our infectious compartment. By using our disease-free equilibrium equations, we are able to calculate our $\mathscr{R}_0$ equation (detailed in Appendix A.3):

$$\mathscr{R}_0 = \frac{\beta\mu_1 q(a(t)(1 - \frac{\mu_1}{r}) + \frac{\mu_1}{r})}{\omega r(\beta h(\frac{\mu_1}{r} - 1) + \beta\mu_2(\frac{\mu_1}{r} - 1) - \beta q(\frac{\mu_1}{r} - 1))} \tag{5}$$

3.4 Sensitivity Analysis

Sensitivity analysis determines the maximum impact of each parameter on the basic reproduction number equation. This process is calculated by performing the partial derivative on the $\mathscr{R}_0$ equation (5) with respect to each parameter value, and substituting the values for the remaining parameter variables. Below is the general equation to calculate sensitivity analysis:

$$S_\lambda = \frac{\frac{\Delta \mathscr{R}_0}{\mathscr{R}_0}}{\frac{\Delta x}{x}} = \frac{\lambda}{\mathscr{R}_0} \cdot \frac{\partial \mathscr{R}_0}{\partial \lambda}$$

where λ is a parameter in the quantity $\mathscr{R}_0$.

Utilizing MatLab (Appendix B.6), we were able to automate the calculation process, giving us the corresponding sensitivity analysis for each parameter variable.

Parameter	S_A
μ_1	**8.3513**
μ_2	**5.2819**
q	-3.5962
ω	-0.7923
σ	0.0000
r	-2.5054
ϕ	0.4029
β	0.0000
h	**5.2819**
a	0.9400

Table 2: Sensitivity Analysis

The larger the sensitivity analysis value, the higher the impact the parameter has on our basic reproduction number equation. The highlighted values (μ_1, μ_2, and h) have the largest sensitivity analysis values, and have the most impact on our basic reproduction number equation, respectively.

The natural death rate of corals (μ_1) represents the largest impact, and rightfully so, with a sensitivity analysis value of 8.3513. Due to the dynamics between corals, algal turfs, and macroalgae, the death of corals directly impacts algal turfs. However, the natural death accounts for all factors of coral deaths, including but not limited to bleaching, disease, damage, and so forth. The more corals that die, the more surface area get converted into algal turfs and subsequently gives way for algal turfs to convert into macroalgae. As such, this rate carries the greatest impact on our overall basic reproduction number equation.

The natural death rate of parrotfish (μ_2) and the harvest rate of parrotfish due to fishing (h) both share the second highest sensitivity analysis value of 5.2819. This presents a unique perspective, as the analysis indicates that there is no difference between natural death and hu1man-driven death. Both simply represent the removal of live parrotfish from the ecosystem rather than the means of removal, and as such are equal. This is significant as our model depicts parrotfish as the primary grazers of macroalgae, and we have acknowledged

that macroalgae overgrowth has a negative impact on the ecosystem. When the parrotfish population is adequate, the proportion of macroalgae will be kept in control. However, with the removal of parrotfish from the ecosystem from death or fishing, the macroalgae will have the opportunity to grow unchecked. Thus, the impact of overfishing parrotfish will undeniably affect the dynamics of the ecosystem, and will allow macroalgae to dominate while corals whither away.

Since the coral death rate (μ_1) had the largest influence on $\mathscr{R}_0$, we wanted to observe how modify the value of μ_1 would affect the harvesting threshold.
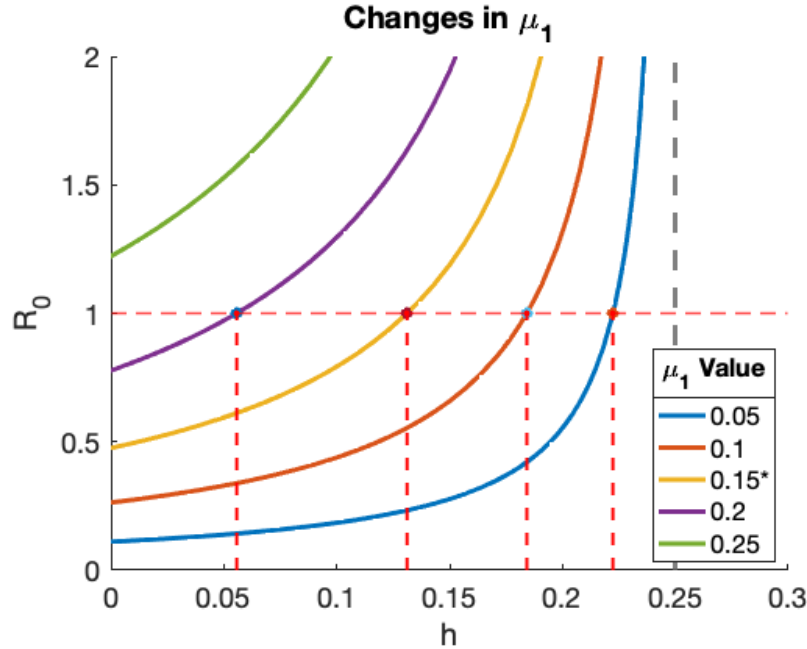

Figure 5: Changes in μ_1

μ_1	h_{TH}
0.05	0.223
0.1	0.1842
0.15	0.1312
0.2	0.0557
0.25	n/a

Table 3: h_{TH} when $\mathscr{R}_0 = 1$ while μ_1 changes

Figure 5 shows how each curve changes as μ_1 changes. Table 3 shows the values of μ_1 with the respective h_{TH} values when $\mathscr{R}_0 = 1$. Evidently, as μ_1 increases, the harvesting threshold decreases. In other words, more parrotfish is needed for the system to maintain stability. Since the coral proportion is decreasing, the macroalgae proportion would increase and more parrotfish would be needed to control the overgrowth of macroalgae, thus resulting in a lower harvesting threshold (h_{TH}).

4 Harvesting Game Theory

One of the primary objectives of our research is to implement game theory to our model. Game theory is essentially "a theoretical framework to conceive social situations among competing players and produce optimal decision-making of independent and competing actors in a strategic setting."[6]. By taking into account strategies, we can apply game theory to predict outcomes.

In our project, we apply education game theory to the harvesting rate of parrotfish, h. Our goal is to predict the best strategy for an individual's choice to harvest (h) in response to the proportion that the population is harvesting parrotfish (h_{pop}). As such, we adapt the concept of education game theory and apply it to our Game of Harvesting.

4.1 Harvesting Threshold

From the basic reproduction number, we are able to obtain the harvesting threshold (h_{TH}), which we defined as the proportion of parrotfish that can be harvested in order for macroalgae growth to maintain stability in the ecosystem.

When $\mathscr{R}_0 = 1$,

$$h_{TH} = q - \mu_2 + \frac{\mu_1 q(a(t)\mu_1 - a(t)r - \phi\mu_1)}{\omega r(r - \mu_1)}$$

Furthermore, we are able to plot our harvesting threshold against our $\mathscr{R}_0$ equation, giving us the figure below.
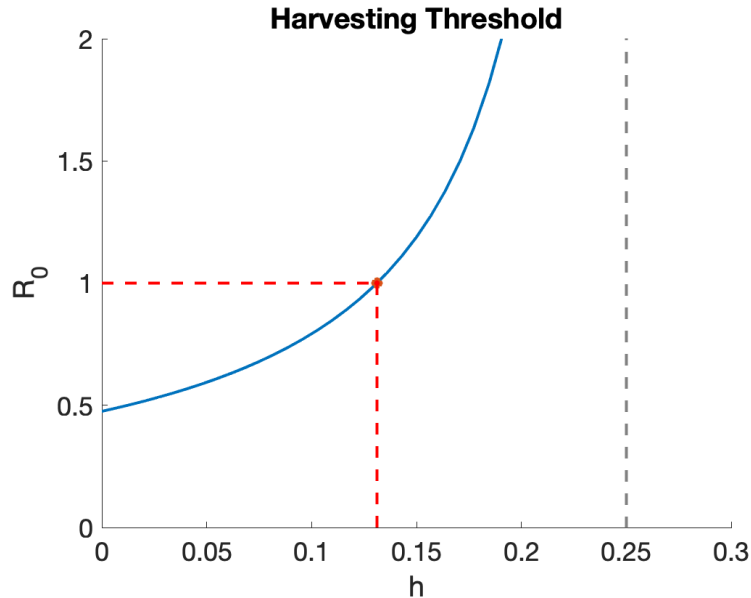

Figure 6: Harvesting Threshold

Figure 6 shows that when $\mathscr{R}_0 = 1$, $h = 0.1312$. This point represents the harvesting threshold, which we defined as the proportion of parrotfish that can be harvested in order

for macroalgae growth to maintain stability in the ecosystem. According to Drieche and Wattmough[5], when $\mathscr{R}_0 < 1$ (i.e. any point below the threshold), the system will be stable. Similarly, when $\mathscr{R}_0 > 1$ (i.e. any point above the threshold), the system will be unstable. Applying this theorem to our model, we obtain

$$h_{pop} < h_{TH} : \text{Macroalgae growth is stable}$$
$$h_{pop} > h_{TH} : \text{Macroalgae growth is unstable.}$$

4.2 Expected Payoff

In game theory, an expected payoff is an equation representing the cost of the player's decision. According to our game, an individual's payoff to harvest is given by

$$E(h, h_{pop}) = -hC^h - \frac{h_{pop}}{h_{pop} + \mu_2} \cdot \frac{g(P^*)(1-h)M^*}{M^* + T^*} \tag{6}$$

where

Symbol	Definition
C^h	cost for an individual to harvest relative to the cost of coral disease
$\frac{h_{pop}}{h_{pop}+\mu_2}$	the probability that parrotfish will be harvested by the population
$\frac{g(P^*)(1-h)M^*}{M^*+T^*}$	the probability that macroalgae (M) will transition to algal turf (T)

and $h \in [0, 1]$ is the proportion at which an individual can harvest parrotfish.

In order to confirm that a Nash equilibrium exists for our expected payoff equation (6), we must determine the concavity by finding the second partial derivative of our expected payoff equation with respect to h. Thus,

$$\frac{\partial^2 E}{\partial h^2} = \frac{2\omega P^* \mu 2(M^* + T^*)^2(\mu_1 + 1)}{\beta(h(M^* + T^*) + \mu_2(M^* + T^*))^3}.$$

Since $\frac{\partial^2 E(h,h_{pop})}{\partial h^2} > 0$, $E(h, h_{pop})$ is a convex function that achieves a maximum value at $h = 0$ and $h = 1$. Furthermore, we can determine the best strategy for an individual based on the results of

$$\Delta E = E(1, h_{pop}) - E(0, h_{pop}),$$

where if

$$\Delta E > 0 : \text{Harvest}$$
$$\Delta E < 0 : \text{Do not harvest.}$$

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4.3 Nash Equilibrium

The Nash equilibrium, named after mathematician John Nash, is a decision-making theorem within game theory that states a player can achieve the desired outcome by not deviating from their initial strategy, and thus, each player's strategy is optimal when considering the decision of other players[3].

Since the maximum is obtained at $h = 0$ or $h = 1$, we are able to find the Nash equilibrium (h_{NE}) by setting our payoff equations equal to each other:

$$E(0, h_{pop}) = E(1, h_{pop})$$

By substituting in $E(0, h_{pop})$ and $E(1, h_{pop})$, we create the following equation:

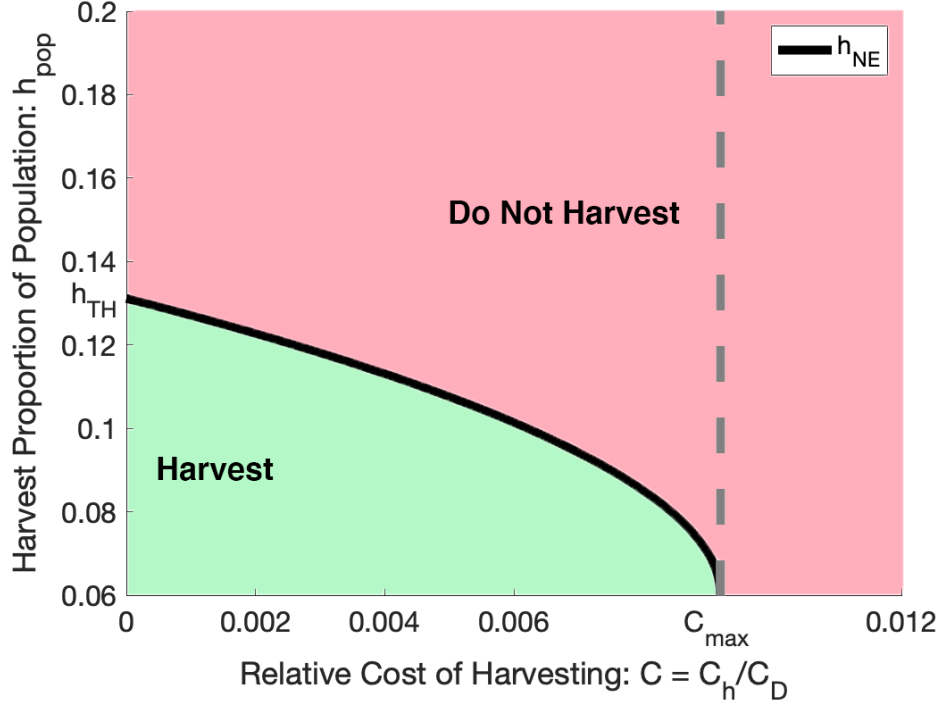$$\frac{h_{pop}}{h_{pop} + \mu_2} \cdot \frac{g(P^*)(1-h)M^*}{M^* + T^*} = C^h.$$

Figure 7: Nash Equilibrium Graph

Figure 7 represents an individual's best strategy based on the relative cost of harvesting, C^h and the harvest proportion of the population, h_{pop}. The graph reveals that an individual's best strategy reaches a maximum relative cost at 0.009. That is to say that an individual should not harvest past a relative cost of 0.009. According to our harvesting game theory, as the relative cost of fishing increases, the harvesting Nash equilibrium decreases until it reaches the maximum cost. As such, as the the relative cost of harvesting increases, the harvest proportion of the population decreases, and by virtue of this analysis, the individual should also harvest less.

5   Discussion

Our model was adopted from Blackwood, Hastings, and Mumby (2010) to study the effects of overfishing on Guam's coral reef ecosystems. In order to apply this model to Guam's coral reef ecosystem, we used several parameters based on the available data for Guam. The other parameter values utilized were models that were adopted from Blackwood, Hastings, and Mumby (2010). From our analysis, there were several parameters that had an impact on the dynamics of our model. The parameter to account for seasonal changes, a_0, showed a direct proportion to macroalgae growth. As a_0 increases, the rate that macroalgae overgrows on coral increases as well. The harvesting rate h exhibited a similar behavior. A higher harvesting rate resulted in an increased dominance of macroalgae in the ecosystem. Alternatively, the rate that macroalgae spread vegetative over algal turfs, ϕ, showed a decrease in the proportion of macroalgae and an increase in algal turfs, and subsequently corals.

Through basic reproduction number, it revealed that the harvesting threshold was approximately 0.131157, meaning if more than 13.1157% of the parrotfish population was harvested, the macroalgae growth will be unstable. Through further analysis of the basic reproduction number, we determined what parameters made an influence on our $\mathscr{R}_0$ and to what extent. Furthermore, it tells us how these parameters affect the harvesting threshold. We found that the coral death rate (μ_1) had the biggest influence and increasing the coral death rate in $\mathscr{R}_0$ would result in a smaller harvesting threshold. As μ_1 increased, the harvesting threshold decreased to the endemic case of the ecosystem, where macroalgae growth is unstable. Additionally, the parrotfish natural death rate (mu_2) and harvesting rate (h) had the second biggest influence on $\mathscr{R}_0$.

Through harvesting game theory, we found that harvesting parrotfish was the best strategy so long as the harvest proportion of the population and relative cost were within the harvesting threshold line. We concluded that as the relative cost of fishing increases, the harvesting threshold decreases until it reaches the maximum relative cost.

6   Future Research

Due to the limited nature of available sources, certain parameters were adapted from other scholarly articles. To further continue this research, we intend to fully utilize local (Guam) parameter values in our model. Furthermore, we intend to introduce more elements of a coral reef ecosystem, such as other types of plant and aquatic life, into our model to more accurately represent a realistic coral reef ecosystem. Lastly, we intend to extend the application of game theory to the rate at which macroalgae spread vegetative over algal turfs, ϕ, to determine the best strategy for control measures such as coastal and/or algal cleanups.

7   Acknowledgements

Appendix

A   Step-by-Step Calculations

A.1   Disease Free Equilibrium

The disease-free equilibrium occurs when we have $(C, M, T, P) = (C^0, 0, T^0, P^0)$.
Solving for T^0, let $\frac{dT}{dt} = 0$:

$$0 = \mu_1 C^0 + \frac{g(P)M^0}{M^0 + T^0} - T(rC^0 + \phi M^0)$$

$$rC^0 T^0 = \mu_1 C^0$$

$$T^0 = \frac{\mu_1}{r}$$

Solving for P^0, let $\frac{dP}{dt} = 0$:

$$0 = qP^0 \left(1 - \frac{P^0}{\beta C^0} \right) - P^0(h + \mu_2)$$

$$0 = P \left(q \left(1 - \frac{P^0}{\beta C^0} \right) - h - \mu_2 \right)$$

$$0 = q - \frac{qP^0}{\beta C^0} - h - \mu_2$$

$$-\frac{qP^0}{\beta C^0} = h + \mu_2 - q$$

$$qP^0 = -\beta C^0(h + \mu_2 - q)$$

$$P^0 = \frac{-\beta C^0(h + \mu_2 - q)}{q}$$

Solving for C^0, let $\frac{dC}{dt} = 0$:

Since $C + M + T = 1$, then

$$C^0 + M^0 + T^0 = 1$$

$$C^0 + T^0 = 1$$

$$C^0 = 1 - T^0$$

$$= 1 - \frac{\mu_1}{r}$$

After inputting C^0 into P^0, we obtain the disease free equilibrium at

$$(C^0, M^0, T^0, P^0) = \left(1 - \frac{\mu_1}{r}, 0, \frac{\mu_1}{r}, -\frac{\beta(1 - \frac{\mu_1}{r})(h - \mu_2 - q)}{q} \right).$$

A.2 Endemic Equilibrium

First, we solved each differential equation in terms of M:

- Calculating T^* :

$$\frac{dT}{dt} = \mu_1 C + \frac{g(P)M}{M+T} - T(rC + \phi M)$$

$$0 = \mu_1 C + \frac{g(P)M}{M+T} - T(rC + \phi M)$$

$$0 = \mu_1 C + \frac{g(P)M}{M+T} - rTC + \phi TM)$$

The term ϕTM cancel out with the similar term from the $\frac{dM}{dt}$ equation (3). Thus, we are left with:

$$0 = \mu_1 C + a(t)MC - rTC$$
$$rTC = \mu_1 C + a(t)MC$$
$$T = \frac{\mu_1 + a(t)M}{r}$$

Solving for T when $\frac{dT}{dt} = 0$, we have:

$$T^* = \frac{\mu_1 + a(t)M^*}{r}$$

- Calculating C^* : Since $C^* + T^* + M^* = 1$, then

$$\frac{dC}{dt} = 1 - T^* - M^*$$

Having already solved for T^*, we are able to substitute in T^* to find C^*:

$$\frac{dC}{dt} = 1 - \frac{\mu_1 + a(t)M^*}{r} - M^*$$

- Calculating P^* :

$$\frac{dP}{dT} = qP\left(1 - \frac{P}{\beta C}\right) - P(h + \mu_2)$$

$$0 = qP\left(1 - \frac{P}{\beta C}\right) - P(h + \mu_2)$$

$$P(h + \mu_2) = qP\left(1 - \frac{P}{\beta C}\right)$$

$$\frac{(h + \mu_2)}{q} = \left(1 - \frac{P}{\beta C}\right)$$

$$\frac{P}{\beta}C = 1 - \frac{h + \mu_2}{q}$$

$$P^* = \beta C^*\left(\frac{q - (h + \mu_2)}{q}\right)$$

17

Having already solved for C^*, we are able to substitute in C^* to find P^* in terms of M^*:

$$P^* = \beta \left(1 - \left(\frac{\mu_1 + a(t)M^*}{r} + M^* \right) \right) \left(\frac{q - (h + \mu_2)}{q} \right)$$

- Calculating M^* :

$$\frac{dM}{dt} = (a(t)C + \phi T)M - \frac{g(P)M}{M + T}$$

$$0 = a(t)CM + \phi TM - \frac{g(P)M}{M + T}$$

$$0 = a(t)CM + \phi TM - \frac{\frac{\omega P}{\beta}M}{M + T}$$

$$0 = a(t)CM + \phi TM - \frac{\omega PM}{\beta(M + T)}$$

$$0 = a(t)CM\beta(M + T) + \phi TM\beta(M + T) - \omega PM$$

$$M = \frac{\omega P}{\beta(a(t)C + \phi T)} - T$$

Thus, we find that M^* is

$$M^* = \frac{\omega P^*}{\beta(a(t)C^* + \phi T^*)} - T^*$$

By substituting all our E^* equations into M^* (i.e. P^*, T^*, and C^*), we are able to find an equation in terms of parameters, which can then be substituted into calculate a value. So, we get

$$M^* = \frac{\beta\omega(1 - \frac{\mu_1 + a(t)M^*}{r} - M^*)(q - h - \mu_2)}{\beta q(\frac{a(t)(r - \mu_1 - a(t)M^* - rM^*)}{r}) + \frac{\phi(\mu_1 + a(t)M^*)}{r})} - \frac{\mu_1 + a(t)M^*}{r}$$

$$= \frac{\omega(1 - \frac{\mu_1 + a(t)M^*}{r} - M^*)(q - h - \mu_2)}{q(\frac{a(t)(r - \mu_1 - a(t)M^* - rM^*)}{r}) + \frac{\phi(\mu_1 + a(t)M^*)}{r})} - \frac{\mu_1 + a(t)M^*}{r}$$

$$= \frac{r\omega(q - h - \mu_2)((r - \mu_1) - (a(t) + r)M^* - (\mu_1 + a(t)M^*q((a(t)r - a\mu_1 + \phi\mu_1)}{rq((a(t)r - a(t)\mu_1 + \phi\mu_1) + (-(a(t))^2 - a(t)r + \phi a(t))M^*)}$$

$$+ \frac{(-(a(t))^2 - a(t)r + \phi a(t))M^*)}{rq((a(t)r - a(t)\mu_1 + \phi\mu_1) + (-(a(t))^2 - a(t)r + \phi a(t))M^*)}$$

$$\text{L.H.S} = rq(a(t)r - a(t)\mu_1 + \phi\mu_1)M^* + rq(-(a(t))^2 - a(t)r + \phi a(t))(M^*)^2$$

$$\text{R.H.S} = r\omega(q - h - \mu_2)(r - \mu_1) - r\omega(q - h - \mu_2)(a(t) + r)M^* - q\mu_1(a(t)r - a(t)\mu_1 + \phi\mu_1)$$
$$- q(a(t)(a(t)r - a(t)\mu_1 + \phi\mu_1) + \mu_1(-(a(t))^2 - a(t)r + \phi a(t)))M^*$$
$$- a(t)q(-a^2 - a(t)r + \phi a(t))(M^*)^2$$

where $L.H.S = R.H.S$.

By isolating all M^* terms on one side, we obtain

$$(M^*)^2[a(t)q(a + r)(-a(t) - r + \phi)]+$$
$$M^*[q(a(t) - a(t)\mu_1 + \phi\mu_1)(a(t) + r) + r\omega(q - h - \mu_2)(a(t) + r)]+$$
$$[-r\omega(q - h - \mu_2)(r - \mu_1) + q\mu_1(a(t)r - a(t)\mu_1 + \phi\mu_1]$$
$$= 0$$

Thus, the general equation of M^* is

$$j = (a(t)q - 2a(t)r + r\phi) - q(r^2 + a(t)^3)$$
$$k = a(t)q(r(r - 2\mu_1 + a(t)) - 2\mu_1(a(t) + \phi)) + r(q(\phi\mu_1 + r\omega)-$$
$$\omega(hr + a(t)\mu_2 + r\mu_2)$$
$$n = -qr^2\omega + qr\mu_1\omega + hr^2\omega - hr\mu_1\omega + r^2\mu_2\omega - r\mu_1\mu_2\omega + a(t)qr\mu_1-$$
$$a(t)q\mu_1^2 + q\phi\mu_1^2$$

where j, k, and n are values in the general quadratic equation:

$$\frac{-k \pm \sqrt{k^2 - 4jn}}{2j}$$

A.3 Basic Reproduction Number: $\mathscr{R}_0$

Firstly, we will set-up our $\mathscr{F}$ and $\mathscr{V}$ matrices, which are:

$$\mathscr{F} = \begin{bmatrix} a(t)CM + \phi MT \end{bmatrix}$$
$$\mathscr{V} = \begin{bmatrix} \frac{g(P)M}{M+T} \end{bmatrix}$$

Since M is considered our infected compartments, we will find the partial derivatives with regards to M using Jacobian Matrices:

$$\mathscr{F} = \begin{bmatrix} aCM + \phi MT \end{bmatrix} \longrightarrow F = \begin{bmatrix} a(t)C^0 + \phi T^0 \end{bmatrix}$$

$$\mathscr{V} = \begin{bmatrix} \frac{g(P)M}{M+T} \end{bmatrix} \longrightarrow V = \begin{bmatrix} \frac{g(P)T^0}{(M^0+T^0)^2} \end{bmatrix}$$

(Note: Since we are simply using a 1×1 $\mathscr{F}$ and $\mathscr{V}$, performing a Jacobian matrix operation

is equivalent to performing a single partial derivative operation with respect to M.) After calculating for F and V, we will calculate the inverse of V by taking the reciprocal of V:

$$V = \left[\frac{g(P)T^0}{(M^0+T^0)^2} \right] \longrightarrow V^{-1} = \left[\frac{aC^0T^0+\phi(T^0)^2}{g(P^0)} \right]$$

Our next step is to calculate FV^{-1}, which is found by matrix multiplication:

$$FV^{-1} = \left[a(t)C^0 + \phi T^0 \right] \cdot \left[\frac{aC^0T^0+\phi(T^0)^2}{g(P^0)} \right]$$

$$= \left[\frac{(a(t)C^0T^0+\phi(T^0)^2)(a(t)C^0T^0)}{g(P^0)} \right]$$

Lastly, we are able to calculate the eigenvalues of our FV^{-1} result:

$$\det(FV^{-1} - \lambda I) = \left[\frac{(a(t)C^0T^0+\phi(T^0)^2)(a(t)C^0T^0)}{g(P^0)} \right] - \lambda \begin{bmatrix} 1 \end{bmatrix}$$

$$= \left[\frac{(a(t)C^0T^0+\phi(T^0)^2)(a(t)C^0T^0)}{g(P^0)} - \lambda \right]$$

$$= \frac{(a(t)C^0T^0 + \phi(T^0)^2)(a(t)C^0T^0)}{g(P^0)} - \lambda$$

To calculate the eigenvalues, we must set the solution of $\det(FV^{-1} - \lambda I) = 0$, which gives us:

$$\lambda = -\frac{(a(t)C^0T^0 + \phi(T^0)^2)(a(t)C^0T^0)}{g(P^0)}$$

Typically, $\mathscr{R}_0$ will be the largest of all eigenvalues, however since we only have one eigenvalue, the singular eigenvalue will be our $\mathscr{R}_0$. After substituting in C^0, T^0, and P^0, our $\mathscr{R}_0$ is

$$\mathscr{R}_0 = \frac{\beta\mu_1 q(a(t)(1 - \frac{\mu_1}{r}) + \frac{\mu_1}{r})}{\omega r(\beta h(\frac{\mu_1}{r} - 1) + \beta\mu_2(\frac{\mu_1}{r} - 1) - \beta q(\frac{\mu_1}{r} - 1))}$$

B   MatLab Scripts

B.1   Static Compartment Model Visualization

This script represents our MatLab implementation of visualizing our compartment model and dynamics using our known and estimated parameters. The code implements ODE45 in order to calculate our system of differential equations, and plots the results:

```
1  %% Compartment - Single View - System of Differential Equations
2  clear; % Clears workspace
3  clc; % Clears Command Window
4
5  %---------------------------------------------
6  % Parameter Values
7  mu1 = 0.15; % mortality rate of coral reefs
8  mu2 = 0.22; % natural death rate of parrotfish
9  q = 0.47; % intrinsic growth rate for parrotfish
10 omega = 1; % %maximum grazing intensity
```

```matlab
11 sigma = 0.01; % rate that parrotfish bite corals
12 r = 0.5; % rate that coral recruit to overgrow algal turfs
13 phi = 0.8; %rate that macroalgae spread vegetative over algal turfs
14 beta = 1; % carrying capacity
15
16 a0 = 0.99; % rate that coral is overgrown by macroalgae
17 h = 0.317429; %<----CONTROL VARIABLE FOR GAME THEORY
18
19 %grazing intensity 'g'
20 g = @(P) (omega*P)/beta;
21
22 %sin function of
23 a = @(t) abs((a0*(9*sin(pi*t)+1))/(10));
24 %----------------------------------------------
25
26 %----------------------------------------------
27 % Compartment Initial Conditions
28 C = 3/5;
29 P = 3/4;
30 T = 1/5;
31 M = 1/5;
32 Prop_Total = C + T + M;
33 IC = [C, P, T, M, Prop_Total];
34 %----------------------------------------------
35
36 % dC/dt = rTC + sigmaPC - C(aM + d)
37 % dP/dt = qP(1-P/betaC) - (h + mu)P
38 % dT/dt = dC + (g(P)M)/(M + T) - (rC + phiM)T
39 % dM/dt = aMC + phiMT - (g(P)M)/(M + T)
40 %
41 % C = y(1), P = y(2), T = y(3), M = y(4), C+T+M = y(5)
42 f = @(t,y) [r*y(3)*y(1) + sigma*y(2)*y(1) - y(1)*(a(t)*y(4) + mu1),
43         q*y(2)*(1-(y(2)/(beta*y(1)))) - (h+mu2)*y(2),
44         mu1*y(1) +  (g(y(2))*y(4))/(y(4)+y(3)) - (r*y(1) + phi*y(4))*y(3),
45         a(t) * y(4)*y(1) + phi*y(4)*y(3) - (g(y(2))*y(4))/(y(4)+y(3)),
46         y(1)+y(3)+y(4)];
47
48 [t,ya] = ode45(f, [0 5], IC);
49
50 figure
51 hold on
52 plot(t, ya(:,1), '+-.', 'Color', '#FFC996', 'Linewidth', 2.5)
53 plot(t, ya(:,2), 'x-.', 'Color', '#4974A5', 'Linewidth', 2.5)
54 plot(t, ya(:,3), 'o-.', 'Color', '#BDD2B6', 'Linewidth', 2.5)
55 plot(t, ya(:,4), '*-.', 'Color', '#CF0000', 'Linewidth', 2.5)
56 %legend('Coral (C)', 'Algal Turf (T)', 'Macroalgae (M)')
57 set(gca, 'FontSize',18);
58 ylim([0 1]);
59 legend('Coral (C)', 'Parrotfish (P)', 'Algal Turf (T)', 'Macroalgae (M)')
60 %text(0.25,0.05,txt, 'FontSize', 18);
61 xlabel('Time (Year)')
62 ylabel('Proportion of Population')
```

B.2 Dynamic Compartment Model Visualization

Similarly to our Static Compartment Model Visualization (Appendix B.1) script, this script visualizes and models our system of differential equations using ODE45. However, this differs from the previous in that it allows for parameter simulations, and subsequently able to create a frame-by-frame animation of the changes:

```matlab
%% Compartment - Animation View - System of Differential Equations
clear; % Clears workspace
clc; % Clears Command Window

% Parameter Values
mu1 = 0.15; % mortality rate of coral reefs
mu2 = 0.22; % natural death rate of parrotfish
q = 0.47; % intrinsic growth rate for parrotfish
omega = 1; % %maximum grazing intensity
sigma = 0.01; % rate that parrotfish bite corals
r = 0.5; % rate that coral recruit to overgrow algal turfs
phi = 0.8; %rate that macroalgae spread vegetative over algal turfs
beta = 1; % carrying capacity

a0 = 0.99; % rate that coral is overgrown by macroalgae
h = 0.1; %<----CONTROL VARIABLE FOR GAME THEORY

%grazing intensity 'g'
g = @(P) (omega*P)/beta;

%sin function of
a = @(t) abs((a0*(9*sin(pi*t)+1))/(10));
%--------------------------------------------

%--------------------------------------------
% Compartment Initial Conditions
C = 1/4;
P = 3/4;
T = 1/4;
M = 1/2;
Prop_Total = C + T + M;
IC = [C, P, T, M, Prop_Total]; %Initial Conditions array
%--------------------------------------------

% System of Differential Equations
    f = @(t,y) [r*y(3)*y(1) + sigma*y(2)*y(1) - y(1)*(a(t)*y(4) + mu1),
        q*y(2)*(1-(y(2)/(beta*y(1)))) - (h+mu2)*y(2),
        mu1*y(1) +  (g(y(2))*y(4))/(y(4)+y(3)) - (r*y(1) + phi*y(4))*y(3),
        a(t) * y(4)*y(1) + phi*y(4)*y(3) - (g(y(2))*y(4))/(y(4)+y(3)),
        y(1)+y(3)+y(4)];

    % Solve using ODE45
    [t,ya] = ode45(f, [0 5], IC);
    const_t = t; % constant used since t changes each time ode45 is
    calculated
```

```matlab
46  for i = 1:length(const_t)
47      phi = (length(const_t)+1-i)/length(const_t); %variable to animate
48
49      % System of Differential Equations
50      f = @(t,y) [r*y(3)*y(1) + sigma*y(2)*y(1) - y(1)*(a(t)*y(4) + mu1),
51          q*y(2)*(1-(y(2)/(beta*y(1)))) - (h+mu2)*y(2),
52          mu1*y(1) +  (g(y(2))*y(4))/(y(4)+y(3)) - (r*y(1) + phi*y(4))*y(3),
53          a(t) * y(4)*y(1) + phi*y(4)*y(3) - (g(y(2))*y(4))/(y(4)+y(3)),
54          y(1)+y(3)+y(4)];
55
56      % Solve using ODE45
57      [t,ya] = ode45(f, [0 5], IC);
58
59      % Plot
60      txt = ['phi = ' num2str(phi)]; % shows value of param value at
    iteration
61
62      fig = figure;
63      hold on
64      plot(t, ya(:,1), '+-.', 'Color', '#FFC996', 'Linewidth', 2.5)
65      plot(t, ya(:,2), 'x-.', 'Color', '#4974A5', 'Linewidth', 2.5)
66      plot(t, ya(:,3), 'o-.', 'Color', '#BDD2B6', 'Linewidth', 2.5)
67      plot(t, ya(:,4), '*-.', 'Color', '#CF0000', 'Linewidth', 2.5)
68
69      set(gca, 'FontSize',18); % sets axis & legend font size to 18
70      ylim([0 1]); % sets y-axis limit to always be 0-1
71      legend('Coral (C)','Parrotfish (P)','Algal Turf (T)','Macroalgae (M)')
72      text(0.25,0.05,txt, 'FontSize', 18); % displays text on plot
73
74      xlabel('Time (Year)')
75      ylabel('Proportion of Population')
76
77      % automatically save figure into root directory (where this .m file is
78      % stored)
79      fname = append('Frame-', num2str(i)); %file name of current iteration
80      saveas(fig, fname, 'png'); %save figure as .png
81  end
```

B.3   Disease Free Equilibrium

This script utilizes MatLab's symbolic toolbox feature to calculate our disease free equilibrium equations:

```matlab
1  %% Disease Free Equilibrium
2  clear; % Clears workspace
3  clc; % Clears Command Window
4
5  %---------------------------------------------
6  % Symbolic Definitions
7  syms C P T M mu1 mu2 q omega sigma beta r h phi g a t
8  % g = g(P), a = a(t)
9
```

```
10 g = @(P) (omega*P)/beta; %grazing intensity 'g'
11
12 %a = @(t) abs((0.9*(9*sin(pi*t)+1))/(10)); %sin function of a(t)
13 %-------------------------------------------
14
15 M_0 = 0;
16
17 dTdt = mu1*C + (g(P)*M_0)/(M_0+T) - T*(r*C + phi*M_0);
18 T_0 = solve(dTdt == 0, T);
19
20 C_0 = 1 - T_0;
21
22 dPdt = q*P*(1-(P/(beta*C))) - P*(h+mu2);
23 P_0 = solve(dPdt == 0, P);
24 P_0 = subs(P_0, C, C_0);
```

B.4 Basic Reproduction Number: $\mathscr{R}_0$

Using our disease free equilibrium equations (Appendix B.3), we are then able to set-up and calculate our basic reproduction number ($\mathscr{R}_0$), which depicts the equilibrium of the system:

```
1 %% R0
2 %Note: RUN 'DISEASE FREE EQUILIBRIUM' SECTION FIRST
3
4 %script F
5 sF = [a*C*M + phi*T*M];
6 F = jacobian(sF, [M]); % jacobian matrix
7 F = subs(F, T, T_0);
8
9 %script V
10 sV = [(g(P)*M)/(M+T)];
11 V = jacobian(sV, [M]);
12 V = subs(V, M, M_0);
13
14 %eigenvalues of F*V^-1
15 eigens = eig(F * inv(V));
16
17 % basic reproduction number
18 R0 = eigens(1);
19 R0 = subs(R0, T, T_0);
20 R0 = subs(R0, C, C_0);
21 R0 = subs(R0, P, P_0(2));
```

B.5 Threshold

This script uses our disease free equilibrium (Appendix B.3) and our basic reproduction number (Appendix B.4) to calculate our harvesting rate threshold, beyond which the system would become unstable:

```
1  %% Threshold
2  % Note: MUST RUN 'DISEASE FREE EQUILIBRIUM' & 'R0' SECTION FIRST
3  param_array = [mu1, mu2, q, omega, sigma, r, beta, a, phi]; %when a0 =
4  % 0.99
5  param_values = [0.15, 0.22, 0.47, 1, 0.01, 0.5, 1, 0.5, 0.8]; %a(t) = 0.5
6
7  hi_equation = R0;
8  hi_value = solve(R0 == 1, h);
9
10 for i = 1:length(param_array)
11     hi_equation = subs(hi_equation, param_array(i), param_values(i));
12     hi_value = subs(hi_value, param_array(i), param_values(i));
13 end
14
15 hi_point = [double(hi_value), 1];
16
17 h_var = 0:0.001:1;
18
19 figure
20 hold on
21 fplot(hi_equation, [0 1], 'Linewidth', 2)
22 plot(hi_point(1), hi_point(2), 'o', 'MarkerFaceColor', 'r', 'Linewidth',
       2)
23 plot([hi_point(1), hi_point(1)], [0, hi_point(2)], 'r--', 'Linewidth', 2)
24 plot([0, hi_point(1)], [hi_point(2), hi_point(2)], 'r--', 'Linewidth', 2)
25 xlim([0 0.3]);
26 ylim([0 2]);
27
28 set(gca, 'FontSize',18);
29 title('Harvesting Threshold');
30 xlabel('h')
31 ylabel('R_0')
32 hold off
```

B.6 Sensitivity Analysis

This script analyzes the impact of each parameter on our basic reproduction number equation by taking the partial derivative and substituting the variables with parameter values:

```
1  %% Sensitivity Analysis
2  % Note: MUST RUN 'DISEASE FREE EQUILIBRIUM' & 'R0' SECTION FIRST
3
4  param_array = [mu1, mu2, q, omega, sigma, r, phi, beta, h, a];
5  param_values = [0.15, 0.22, 0.47, 1, 0.01, 0.5, 0.8, 1, 0.1, 0.5];
6  sens_analysis = [];
7
8  for i = 1:length(param_array)
9      R0_diff = diff(R0, param_array(i));
10     %sens_analysis = cat(1, sens_analysis, diff(R0, param_array(i)));
11     for j = 1:length(param_array)
12         R0_diff = subs(R0_diff, param_array(j), param_values(j));
13     end
```

```
14        sens_analysis = cat(1, sens_analysis, double(R0_diff));
15        %subs_ans = cat(1, subs_ans, [param_array(i) double(R0_diff)]);
16  end
```

B.7   Endemic Equilibrium

This script calculates the endemic equilibrium of our system of differential equations:

```
1   %% Endemic Equilibrium
2   clear; % Clears workspace
3   clc; % Clears Command Window
4
5   %------------------------------------------------
6   % Symbolic Definitions
7   syms C P T M mu1 mu2 q omega sigma beta r h phi g a t
8   % g = g(P), a = a(t)
9
10  g = @(P) (omega*P)/beta; %grazing intensity 'g'
11
12  % a = @(t) abs((0.9*(9*sin(pi*t)+1))/(10)); %sin function of a(t)
13  %------------------------------------------------
14
15  %------------------------------------------------
16  % Equation
17  T_E = (mu1 + a*M)/r;
18
19  C_E = 1 - (T+M);
20  C_E = subs(C_E, T, T_E);
21
22  P_E = (beta*C*(q-(h+mu2)))/q;
23  P_E = subs(P_E, C, C_E);
24
25  M_E = (omega*P)/(beta*(a*C+phi*T))-T - M;
26  M_E = subs(M_E, P, P_E);
27  M_E = subs(M_E, C, C_E);
28  M_E = subs(M_E, T, T_E);
29  M_E_equation = solve(M_E == 0, M);
30  %------------------------------------------------
31
32  %------------------------------------------------
33  % Calculates M_E Value by substitution
34  param_array = [mu1, mu2, q, omega, sigma, r, phi, beta, h, a];
35  param_values = [0.15, 0.22, 0.47, 1, 0.01, 0.5, 0.8, 1, 0.1, 0.5];
36
37  M_E_Value = M_E_equation;
38
39  for i = 1:length(param_array)
40      M_E_Value = subs(M_E_Value, param_array(i), param_values(i));
41  end
```

B.8 Game Theory

This script performs calculates and plots our nash equilibrium graph for our harvesting game theory:

```matlab
%% Game Theory
% Note: MUST RUN 'ENDEMIC EQUILIBRIUM' FIRST

param_array = [mu1, mu2, q, omega, sigma, r, phi, beta, a];
param_values = [0.15, 0.22, 0.47, 1, 0.01, 0.5, 0.8, 1, 0.5];

n_e = -C + (h*omega*P*M)/(beta*(h+mu1)*(M+T));
n_e = subs(n_e, P, P_E);
n_e = simplify(n_e);

n_e = subs(n_e, T, T_E);
n_e = simplify(n_e);

n_e = subs(n_e, M, M_E_equation(1));
n_e = simplify(n_e);

for i = 1:length(param_array)
    n_e = subs(n_e, param_array(i), param_values(i));
end

n_e = simplify(n_e, 'Steps', 50);

n_e_solution = solve(n_e == 0, h);
%n_e_solution = solve(n_e == 0, h, 'Real', true)
%n_e_solution = solve(n_e == 0, h, 'IgnoreAnalyticConstraints', true)
%n_e_solution = vpasolve(n_e == 0, h)

hold on
fplot(n_e_solution(3), 'LineWidth', 5, 'Color', '#000000') %sol #3 gives
    nash graph
legend('h_{NE}')

%title("Nash Equilibrium")
xlim([0 0.012])
ylim([0.06 0.2])
set(gca, 'FontSize',16)
xticks([0 0.002 0.004 0.006 0.00913609 0.012])
xticklabels({'0' '0.002' '0.004' '0.006' 'C_{max}' '0.012'})
yticks([0.06 0.08 0.1 0.12 0.131157 0.14 0.16 0.18 0.2])
yticklabels({'0.06' '0.08' '0.1' '0.12' 'h_{TH}' '0.14' '0.16' '0.18' '0.2
    '})
xlabel("Relative Cost of Harvesting: C = C_{h}/C_{D}")
ylabel("Harvest Proportion of Population: h_{pop}")
```

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