

A Mathematical Model of Coral Reef Response to Destructive Fishing Practices with Predator-Prey Interactions

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Abstract

Coral reefs are being degraded by multiple anthropogenic stressors, including excessive and destructive fishing practices. Such activities damage reefs directly, particularly when cyanide and explosives are employed, and deplete reef fishes that keep coral predators and competitors in check. In this work, we focus on the highly problematic corallivore Crown-of-thorns starfish (CoTS), *Acanthaster planci*, and one of its few known predators, the endangered and overfished Humphead wrasse, *Cheilinus undulatus*. We built a system of non-linear ordinary differential equations to model the interactions between coral, wrasse, and CoTS biomasses within the Indonesian province of Raja Ampat. We consider commensalism between wrasse and coral in favor of wrasse, and predator-prey relationships between wrasse and CoTS, and CoTS and coral. We take into account coral damage from illegal, unregulated, and unreported (IUU) fishing and consider constant yield, constant effort, and seasonal wrasse harvesting. Equilibria for the system with and without harvesting are determined, including coexistence equilibria in which all three species persist. We run numerical simulations and conduct sensitivity analyses on key parameters.

Through this work, we hope to provide insight on the extent to which the coral reefs of Raja Ampat can hold up to rising fishing pressure as well as describe a model which can be applied to similar ecosystems.

1 Introduction

Coral reefs form the center of biodiversity in the world's oceans, home to a quarter of all marine life [3]. They provide the nations they flank with an abundance of resources like food fish and medicines. Coral-related tourism generates \$9.6 billion USD worldwide, and play a large role in many Pacific island economies [28]. However, a collection of anthropogenic stressors has arisen which are degrading coral reefs. A 2008 world coral reef status report projected that 15% of all coral reefs are in danger of disappearing within 10-20 years, and 20% within 20-40 years [13] .

Ocean acidification¹ damages the calcium carbonate skeleton of many reef-building hard corals. On the other hand, sea temperatures cause thermal stress in corals, leading to mass bleaching events that have turned once vibrant reefs into pale graveyards. Increased nutrient flow into oceans from terrestrial runoff is implicated in improved survivorship for the larvae of coral competitors and predators [6]. Exacerbating this problem, exploitative fishing practices deplete populations of reef fish that usually keep coral predators and algae in check [10, 13]. To make matters worse, it is well known that illegal and destructive fishing, including blast and poison fishing, directly damage coral reefs [27].

While threats stemming from global climate, like ocean acidification, cannot themselves be mitigated by the actions of one nation, local and regional actions *can* be taken to contribute to coral reef resilience and address such threats as destructive fishing and pollution. Every coral reef is unique in its dynamics (though geographical trends have previously been noted), and it is important that these dynamics inform management strategy development [28].

In this paper, we aim to increase this body of knowledge by focusing on excessive and destructive fishing practices and the resultant disruption of trophic cascades in coral reefs ecosystem. The interactions between three components are mathematically modeled: the coral reef, a problematic corallivore, and a predator of the corallivore which has a commensal relationship with coral. Although this model can be applied to any situation with similar dynamics to those we describe here, we apply our model to Crown-of-thorns starfish and Humphead wrasse interactions within the reefs of the Indonesian province of Raja Ampat.

The structure of the paper is as follows: In Section 2, we provide background information on the ecosystem under study. We then, in section 3, describe the model

¹a result of the ever increasing load of carbon dioxide in the earth's atmosphere

we have built to explore this system. We carry out mathematical analysis on the general ecosystem model in section 4, and on the constant effort harvesting model in Section 5. Section 6 details how we arrived at our estimates for model parameters, which are in then utilized in the simulations explained in Section 7. Section 8 contains results from sensitivity analysis on certain parameters, like constant effort harvest and destruction. Finally, we briefly describe simulations on the seasonal harvest model.

2 The Ecosystem

In this section, we describe the interaction between the three populations and natural ecosystem subject to our study.

2.1 The corallivore: Crown-of-thorns starfish

Crown-of-thorns seastars (*Acanthaster Planci*), herein referred to as CoTS, are coral-livores found in coral reefs throughout the Indo-Pacific ocean [15]. They usually occur at low densities of less than 1 CoTS per hectare. At these low densities, this species acts as a buffer for fast growing corals, allowing for corals with a slower growth rate to propagate, thus contributing to the maintenance of biodiversity. However, when CoTS populations surpass sustainable densities, they pose a great danger to the reefs they inhabit.

CoTS outbreaks ² are amongst the greatest threats to tropical coral reefs world-wide [15]. Outbreaks have been observed to destroy up to 80% of original coral cover, at times resulting in a phase shift wherein coral species composition is altered irreparably [5]. In other cases, outbreaks have completely annihilated the coral reefs they take place in [15]. Previous research has given rise to multiple theories around the main cause for these outbreaks. Some indicate that CoTS outbreaks are a natural part of coral reef ecosystems, but perhaps are occurring more frequently now [5]. Outbreaks may stem from increased nutrient flow into the ocean from terrestrial runoff, which is known to boost algae populations. CoTS larvae, then, experience greater survivorship with the increase in algal food supply, resulting in larger adult populations [6]. Another cause may be the depletion of CoTS predators through overfishing. One study, found a link between CoTS population outbreak occurrence and fishing pressure in Fiji over the span of 15 months [10]. Often, starfish populations plummet

²A CoTS outbreak is defined as the density of CoTS at which their feeding rate surpasses that of coral reef growth. The densities at which these occur range from 15 to 30 starfish per hectare, depending on the location [5] [?] [10]. Outbreaks have been known to last 5-7 years and may occur cyclically.

after an outbreak, having consumed enough coral to affect its own numbers.

CoTS have few natural predators. These include the Triton’s trumpet, the shrimp *Hymenocera*, the worm *Pherecardia striata*, the polyps of *Paracorynactis hoplites*, and the Humphead wrasse. [2, 5, 12, 21]. In this study, we focus on the Humphead wrasse because it is one of the most sought after targets of IUU fishermen and is an inhabitant of coral reefs. A coral reef that contains Humphead wrasse is likely to either currently be experiencing damage from poison and blast fishing or will be experiencing damage from these fishing practices in the future.

2.2 The Corallivore predator: Humphead Wrasse

The Humphead wrasse (*Cheilinus undulatus*) is the largest member of the *Labridae* family, with a maximum length of 2m and weight of 190kg. They are markedly long-lived, with the oldest found to be 32 years old. They reach sexual maturity after 5-7 years and gather in reef drop-offs to spawn nearly daily, in numbers ranging from tens to hundreds - but are low in fecundity. Protogynous fish, males may either develop via sex change from adult females or directly from the juvenile phase [23]. These aspects of wrasse development make them particularly sensitive to fishing pressure, as populations are slow to rebound.

Wrasse inhabit coral reefs throughout the tropical Indo-Pacific ocean. Adults frequent the edges of the reefs they inhabit, hiding in caves during the night, while juveniles stay within the reef, often favoring *Acropora* coral [23]. Wrasse can naturally be found in low densities of 10-20 fish per hectare without fishing pressure and 5-10 fish with, while population sizes are directly and linearly correlated with coral cover [13].

The Humphead wrasse is one of the few known predators of CoTS. That said, CoTS likely make up a small percentage of the wrasse diet. A study found starfish to comprise 3% of the gut contents of 32 wrasse analyzed [24], of which CoTS make up an unknown percentage. Considering the range of sizes for wrasse and natural low density of CoTS, though, wrasse consume a considerable portion of CoTS populations.

C. undulatus is a highly valued commodity in the Live Reef Food Fish Trade (LRFFT) and, as such, is and has been subject to severe over-fishing. To increase harvesting yield, fishermen are known to resort to cyanide fishing, wherein sodium cyanide is released into areas within coral reefs where wrasse are suspected to hide [23]. The stunned fish are then captured and set aside to recover. Blast fishing may also be employed, wherein explosives are set off to stun nearby fish, optimizing them for capture. These practices not only negatively impact already fragile wrasse populations, but also cause great damage to the coral reefs they take place in - an effect we account for in our model. In response, *C. undulatus* was placed on the International Union for Conservation of Nature (IUCN) red list as “endangered” in

the year 2004 and strict limits have been placed on wrasse catch quotas. Despite these measures, illegal, unregulated, and unreported (IUU) fishing practices are known to still be rampant [29].

2.3 The Coral Reefs of Raja Ampat

The Coral Triangle is located in the Indo-Pacific ocean and is home to 45% of all coral species. It is a hotbed of biodiversity, but is also under great peril. Arguably, the heart of the Coral Triangle is Raja Ampat - an Indonesian province. Spanning 45,000 km^2 , Raja Ampat is a smattering of islands flanked by coral reefs home to a number of coral and fish species [19]. Though human inhabitants have subsisted for generations on the bounty of the reefs there, mounting economic pressures have driven local fishermen to engage in illegal fishing practices. IUU is on the rise, placing this precious ecosystem in great danger. Locals claim to hear blasts from blast fishing daily, and it is known that cyanide fishing is still frequently used to capture Humphead wrasse for LRFFT [1]. Raja Ampat, then, is a microcosm of what has been occurring worldwide - predatory fish depletion with the potential to lead to a rise in corallivore population, placing coral reefs in danger.

The model we present in this work was inspired by the situation in Raja Ampat, with data drawn particularly from reports on the Dampier Strait [26]. A study found 90% of a stretch of coral reefs in Raja Ampat to be comprised of hard (Scleractinian) coral [4]. As these species of coral are known-reef builders, and are favored by Humphead wrasse and CoTS, they will be the focus of our study.

3 Model Description and Methodology

The model proposed is a system of three non-linear ordinary differential equations describing biomasses of Humphead wrasse, CoTS, and Scleractinian coral within the Indonesian province of Raja Ampat. While we focus on three specific species and one location, our model is a general one that can be applied to any system with similar dynamics. Once statistical study has been done which focuses on CoTS populations in Fiji, in areas of varying fishing pressure [10]. A relationship was found between the depletion of CoTS predators from harvest, and increases in CoTS biomass. Previous models have been developed which represent situations similar to this one - modeling commensalism, modeling harvest - but none, to our knowledge thus far, have modeled both at once [18].

We define $W(t)$, as Humphead wrasse (*Cheilinus undulatus*) biomass at time t ; $S(t)$, as Crown-of-thorns starfish (*Acanthaster planci*) biomass at time t ; and $C(t)$ as Scleractinian coral biomass at time t . We first build our model based on the ecosystem

without human intervention - i.e. without wrasse harvesting and coral destruction from IUU fishing.

3.1 General Ecosystem Model

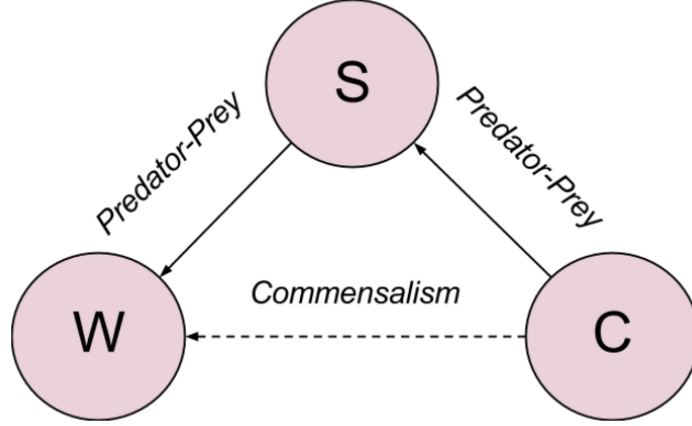


Figure 1: Energy flow diagram for our system, where C is coral, S is CoTS, and W is wrasse.

The Humphead wrasse is one of the few known predators of the CoTS. As mentioned previously, CoTS are not the primary food source for the wrasse, comprising less than 3% of their diet. Thus, density of CoTS does not limit wrasse consumption rate. The more CoTS are available, the more wrasse will eat. The wrasse gain energy from predation on the CoTS at rate α_1 regardless of the CoTS current population size. We classify this predation as Holling Type I (the purple terms in the general ecosystem model refer to this interaction).

Wrasse biomass is largely dependent on coral biomass, but wrasse only offer indirect benefit to coral by predating on corallivores such as CoTS. We classify this interaction as commensalism (the red terms refer to this interaction). The wrasse grow logistically to their own carrying capacity K_1 at rate r_1 . The commensalism relationship between the wrasse and the coral is reflected by the wrasse's ability to grow above that carrying capacity based on the current density of the coral which is represented by the term bC , where b is a conversion factor quantifying the benefit that wrasse derive from coral.

CoTS eat Scleractinian coral almost solely. CoTS population have been found to sharply decline after an outbreak due to the decrease in coral availability. Thus,

CoTS feeding rate is limited by coral population and food processing time. That is, as coral density decreases and CoTS density increases, the feeding rate is capped by CoTS physiology - how quickly they can *possibly* consume coral. Therefore, we classify this predation as Holling Type II (the blue terms in the general ecosystem model refer to this interaction). The coral grows at a logistic rate r_2 to its carrying capacity, K_2 . CoTS predate on the coral at rate γ_1 relative to the current biomass of the coral. Loss of coral from CoTS predation is represented by the term $\frac{\gamma_1 C}{C+q}$.

The CoTS grow logistically to their own carrying capacity, K_3 , at rate r_3 and are able to convert energy from predation on coral into more offspring at rate γ_2 , relative to the coral's density. The conversion function of energy from coral to CoTS is represented by $\frac{\gamma_2 C}{C+q}$. On the other hand, CoTS are predated upon by the Humphead wrasse at rate α_2 .

Figure 1 provides a diagram of the general ecosystem model, while our system of equations is given by:

$$\begin{aligned}\dot{W} &= W \left[r_1 \left(1 - \frac{W}{K_1 + bC} \right) + \alpha_1 S \right], \\ \dot{C} &= C \left[r_2 \left(1 - \frac{C}{K_2} \right) - \frac{\gamma_1 S}{C+q} \right], \\ \dot{S} &= S \left[r_3 \left(1 - \frac{S}{K_3} \right) - \alpha_2 W + \frac{\gamma_2 C}{C+q} \right],\end{aligned}$$

with initial conditions $W(0) = W_0$, $C(0) = C_0$, and $S(0) = S_0$.

3.2 Harvesting Models

After developing the system as it is without human intervention, we consider harvesting. The energy diagram, then, is modified into Figure 2.

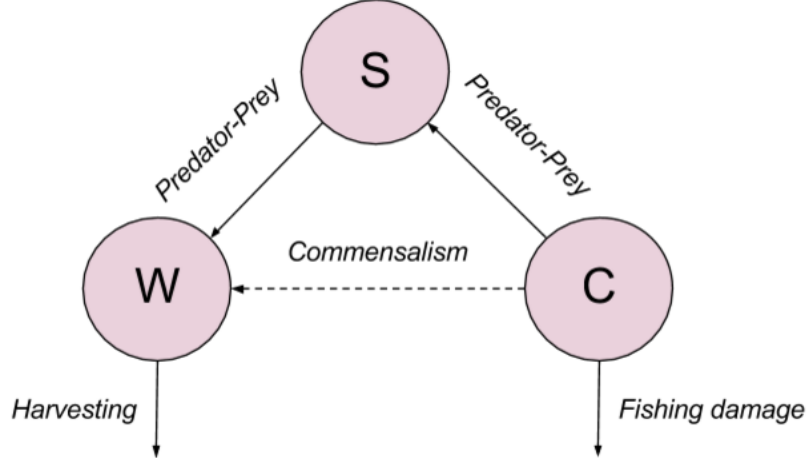


Figure 2: Energy flow diagram for our system, factoring in harvesting and destructive fishing practices.

We denote the rate at which wrasse biomass is harvested at time t by $H(t)$, while $D(t)$ represents the rate of coral destruction by cyanide and blast fishing at time t . Thus, under harvesting and destruction, our system of equations then becomes:

$$\begin{aligned}\dot{W} &= W \left[r_1 \left(1 - \frac{W}{K_1 + bC} \right) + \alpha_1 S \right] - H(t)W, \\ \dot{C} &= C \left[r_2 \left(1 - \frac{C}{K_2} \right) - \frac{\gamma_1 S}{C + q} \right] - D(t)C, \\ \dot{S} &= S \left[r_3 \left(1 - \frac{S}{K_3} \right) - \alpha_2 W + \frac{\gamma_2 C}{C + q} \right],\end{aligned}$$

with initial conditions $W(0) = W_0$, $C(0) = C_0$ and $S(0) = S_0$.

We consider and compare two types of harvesting: constant effort and seasonal. Seasonal harvesting may occur based on weather patterns, as fishers are most able to harvest during fair weather conditions. Seasonality is also used intentionally, in some cases, to allow fish stocks to replenish themselves, resulting in more sustainable harvest.

3.2.1 Constant Effort Harvesting

Under constant effort harvesting, we let $H(t) = H > 0$ - that is, H measures the effort placed into fishing wrasse. On the other hand, we let $D(t) = D > 0$, denoting the rate at which coral are destroyed from cyanide and blast fishing. The wrasse and coral biomass lost in this way, then, is proportional to population size at the time of the harvesting. Note that the general ecosystem model described previously is a special case of the constant effort harvesting model.

3.2.2 Seasonal Harvesting

The weather patterns of Raja Ampat are ruled by its monsoon seasons [18]. Fishing pressure also is ruled by these seasons, as more fishermen are able to harvest during fair ocean weather conditions than during poor conditions. As Humphead wrasse are known to spawn nearly everyday and do not migrate, we can assume that the amount of wrasse biomass that leaves the system at time t via harvesting depends primarily on weather conditions [23].

There are two monsoon seasons in Raja Ampat: southeast and northwest. The southeast monsoon season is characterized by frequent strong winds and upwellings (especially in the Dampier Strait), while the northwest monsoon season is much milder [17]. More fishermen, then, opt to harvest during the former than during the latter. Many villages in Raja Ampat further enforce this harvesting differential with *sasi* - the practice of limiting harvesting for a period of time to allow fish populations to replenish themselves [1]. *Sasi* is enforced during the months of April-September, and lifted October-March, and align with the southeast and northwest monsoon seasons.

We let the harvesting and destruction function $H(t)$ and $D(t)$, then, be sinusoidal functions with period length 1 (for 1 year), where $t = 0$ represents the month of July and $t = 1/11$ represents the month of June. Therefore, our seasonal harvesting and destruction functions are given by

$$H(t) = H_1(\sin(2\pi t - 1.5) + H),$$

and

$$D(t) = D_1(\sin(2\pi t - 1.5) + D),$$

where $H_1 = eH$ and $D_1 = eD$ represent the ranges of harvesting and destruction pressure; and H and D represent the portion of total wrasse and coral biomass removed from the system via harvest and destruction in one year, and are taken from the constant effort harvesting model. It is assumed that destruction and harvesting are directly related, so that the proportional difference between high and low fishing

seasons for both is the same - taken to be parameter e .

Multiplying t by 2π gives the function a cycle length of 1, and subtracting 1.5 translates the function over so that the peak fishing season corresponds with the months of October through March. Similar harvesting functions have been presented before - sine functions modified to match the seasonality described [14].

Table 1 provides our state variable definitions while Table 2 summarizes our model parameters with their respective units.

Table 1: State Variables

| Variable | Description | Units |
|----------|-------------------------------------|-------------------|
| W | Humphead wrasse biomass at time t | $\frac{kg}{km^2}$ |
| C | coral biomass at time t | $\frac{kg}{km^2}$ |
| S | CoTS biomass at time t | $\frac{kg}{km^2}$ |

Table 2: Model Parameters

| Parameter | Description | Units |
|------------|--|-----------------------|
| r_1 | Intrinsic growth rate for wrasse | $\frac{1}{yrs}$ |
| r_2 | Intrinsic growth rate for coral | $\frac{1}{yrs}$ |
| r_3 | Intrinsic growth rate for CoTS | $\frac{1}{yrs}$ |
| K_1 | Wrasse carrying capacity | $\frac{Kg}{km^2}$ |
| K_2 | Coral carrying capacity | $\frac{kg}{km^2}$ |
| K_3 | Starfish carrying capacity | $\frac{kg}{km^2}$ |
| α_1 | Benefit rate from wrasse predation on CoTS | $\frac{kg*yrs}{km^2}$ |
| α_2 | Predation rate from wrasse on CoTS | $\frac{kg*yrs}{km^2}$ |
| γ_1 | Predation rate from CoTS on coral | $\frac{1}{yrs}$ |
| γ_2 | Benefit rate from CoTS predation on coral | $\frac{1}{yrs}$ |
| b | Conversion factor for wrasse benefit from coral | unitless |
| q | CoTS mid-saturation threshold from coral consumption | $\frac{kg}{km^2}$ |
| H | Harvesting function for wrasse | $\frac{1}{yrs}$ |
| D | Function for intrinsic destruction rate for coral | $\frac{1}{yrs}$ |

4 General Ecosystem Model

In this section, we analyze the model without interference from harvesting - and the destruction to coral that comes with it. The aim of this section is to understand the dynamics of the system *naturally*, as it is in the absence of human intervention. We confirm that all three populations can persist in coexistence. This provides a backdrop for the analysis of the system *with* destruction and harvesting, covered in the next section.

Our first model without harvesting satisfies the following system of equations:

$$\dot{W} = W \left[r_1 \left(1 - \frac{W}{K_1 + bC} \right) + \alpha_1 S \right], \quad (4.1a)$$

$$\dot{C} = C \left[r_2 \left(1 - \frac{C}{K_2} \right) - \frac{\gamma_1 S}{C + q} \right], \quad (4.1b)$$

$$\dot{S} = S \left[r_3 \left(1 - \frac{S}{K_3} \right) - \alpha_2 W + \frac{\gamma_2 C}{C + q} \right]. \quad (4.1c)$$

First, we non-dimensionalize system 4.1 in order to simplify analysis - decreasing our twelve existing parameters to eight. If we let $w = \frac{1}{K_1}W$, $c = \frac{1}{K_2}C$, $s = \frac{1}{K_3}S$ and $t = \frac{1}{\gamma_2}\tau$, then we have

$$\begin{aligned} \frac{dw}{d\tau} &= w \left[\frac{r_1}{\gamma_2} \left(1 - \frac{w}{1 + \frac{bk_2}{k_1}c} \right) + \frac{\alpha_1 k_3}{\gamma_2} s \right], \\ \frac{dc}{d\tau} &= c \left[\frac{r_2}{\gamma_2} (1 - c) - \frac{\gamma_1 k_3 s}{\gamma_2 k_2 (\frac{q}{k_2} + c)} \right], \\ \frac{ds}{d\tau} &= s \left[\frac{r_3}{\gamma_2} (1 - s) - \frac{\alpha_2 k_1}{\gamma_2} w + \frac{c}{\frac{q}{k_2} + c} \right]. \end{aligned}$$

The remaining parameters can be grouped into dimensionless non-negative quantities as follows:

$$\begin{aligned} \phi_i &= \frac{r_i}{\gamma_2} \quad \text{for } i = 1, 2, 3; & \beta &= \frac{k_2 b}{k_1}; & p &= \frac{q}{k_2}; \\ \delta_1 &= \frac{k_3 \alpha_1}{\gamma_2}; & \delta_2 &= \frac{\alpha_2 k_1}{\gamma_2}; & \theta &= \frac{\gamma_1 k_3}{\gamma_2 k_2}. \end{aligned}$$

The parameters ϕ_i , for $i = 1, 2$, and 3 are expressions related to the natural intrinsic growth rates for W , C , and S , respectively. The parameter β is analogous to the conversion rate b which is the additional carrying capacity the wrasse gains from the presence of coral being in the environment, while p is related to the mid-saturation threshold from coral consumption relative to the carrying capacity of the coral. The non-dimensional quantity δ_1 represents the increase in wrasse due to consumption of CoTS and δ_2 is the decrease in CoTS from consumption by wrasse. The parameter

θ is modeling the decrease in the coral due to CoTS consumption. These parameters give us the dimensionless system :

$$\frac{dw}{d\tau} = w \left[\phi_1 \left(1 - \frac{w}{1 + \beta c} \right) + \delta_1 s \right], \quad (4.3a)$$

$$\frac{dc}{d\tau} = c \left[\phi_2(1 - c) - \frac{\theta s}{p + c} \right], \quad (4.3b)$$

$$\frac{ds}{d\tau} = s \left[\phi_3(1 - s) + \frac{c}{p + c} - \delta_2 w \right]. \quad (4.3c)$$

Under the dimensionless System 4.3, the population size of the CoTS and coral are divided by their respective carrying capacities (i.e. $c = \frac{C}{K_2}$ and $s = \frac{S}{K_3}$), thus both dimensionless carrying capacities are set to one. Notice that under the dimensionless system, the carrying capacity of the wrasse is one only when coral is not present in the environment. Thus, the wrasse can naturally grow above its carrying capacity by a maximum proportion of β . On the other hand, the CoTS can grow to a carrying capacity that is independent of the coral, this carrying capacity is one. However, when the coral is in the environment, the CoTS can feed on the coral biomass and boost its growth past one.

Next, we conduct algebraic and numerical analysis on our model to determine long-term behavior. We calculate the equilibrium points to determine their stability and existence conditions. This will give us a deeper understanding of the dynamics in this ecosystem.

4.1 Equilibria and Stability

Every equilibrium solution arises as a solution to the system of algebraic equations given by:

$$w \left[\phi_1 \left(1 - \frac{w}{1 + \beta c} \right) + \delta_1 s \right] = 0, \quad (4.4a)$$

$$c \left[\phi_2(1 - c) - \frac{\theta s}{p + c} \right] = 0, \quad (4.4b)$$

$$\text{and} \quad s \left[\phi_3(1 - s) + \frac{c}{p + c} - \delta_2 w \right] = 0. \quad (4.4c)$$

We found at least eight equilibria for System 4.4, five of which always exist, while the existence of the others depends on certain conditions. Let us denote the equilibria

as follows

$$\begin{aligned}
E_0 &= (0, 0, 0), & E_4 &= (1 + \beta, 1, 0), \\
E_1 &= (1, 0, 0), & E_5 &= \left(\frac{\phi_3(\delta_1 + \phi_1)}{\delta_1\delta_2 + \phi_1\phi_3}, 0, \frac{\phi_1(\phi_3 - \delta_2)}{\delta_1\delta_2 + \phi_1\phi_3} \right), \\
E_2 &= (0, 1, 0), & E_6 &= (0, c_1^*, s_1^*), \\
E_3 &= (0, 0, 1), & E_7 &= (w_2^*, c_2^*, s_2^*).
\end{aligned}$$

In order to analyze the stability of each equilibrium, we calculate the Jacobian matrix of dimensionless System (4.3)

$$J(w, c, s) = \begin{bmatrix} \phi_1 - \frac{2w\phi_1}{1+\beta c} + \delta_1 s & \frac{\phi_1 w^2 \beta}{(1+\beta c)^2} & w\delta_1 \\ 0 & \phi_2 - 2\phi_2 c - \frac{\theta s p}{(p+c)^2} & -\frac{\theta c}{p+c} \\ -\delta_2 s & \frac{s}{p+c} - \frac{sc}{(p+c)^2} & \phi_3 - 2\phi_3 s + \frac{c}{p+c} - \delta_2 w \end{bmatrix} \quad (4.5)$$

We will now carry out an existence and stability analysis for each equilibrium.

4.1.1 Extinction Equilibrium

The trivial equilibrium $E_0 = (0, 0, 0)$ always exists. The Jacobian matrix evaluated at this point is

$$J(E_0) = \begin{bmatrix} \phi_1 & 0 & 0 \\ 0 & \phi_2 & 0 \\ 0 & 0 & \phi_3 \end{bmatrix},$$

with eigenvalues $\lambda_1 = \phi_1, \lambda_2 = \phi_2$ and $\lambda_3 = \phi_3$. Since all three of these eigenvalues are positive, this equilibrium point is unstable.

From a biological perspective, E_0 represents the extinction of the wrasse, coral and CoTS. It is unstable because each species is able to survive in the absence of the other two species.

4.1.2 Coral and CoTS Exclusion Equilibrium

The equilibrium $E_1 = (1, 0, 0)$ always exists. The Jacobian matrix evaluated at E_1 gives:

$$J(E_1) = \begin{bmatrix} -\phi_1 & \phi_1\beta & \delta_1 \\ 0 & \phi_2 & 0 \\ 0 & 0 & -\delta_2 + \phi_3 \end{bmatrix},$$

which has eigenvalues $\lambda_1 = -\phi_1$, $\lambda_2 = \phi_2$ and $\lambda_3 = -\delta_2 + \phi_3$. Since E_1 has one eigenvalue that is always positive, this equilibrium point is always unstable.

Biologically, E_1 represents the extinction of the coral and the CoTS, and survival of wrasse. As wrasse are nearly unable to survive without coral, it makes sense for this point to be unstable.

4.1.3 Wrasse and CoTS Exclusion Equilibrium

The equilibrium $E_2 = (0, 1, 0)$, always exists. The Jacobian matrix evaluated at E_2 is given by:

$$J(E_2) = \begin{bmatrix} \phi_1 & 0 & 0 \\ 0 & -\phi_2 & -\frac{\theta}{1+p} \\ 0 & 0 & \frac{1}{1+p} + \phi_3 \end{bmatrix},$$

which has the eigenvalues $\lambda_1 = \phi_1$, $\lambda_2 = -\phi_2$ and $\lambda_3 = \frac{1}{1+p} + \phi_3$. Because λ_1 and λ_3 are always positive, this equilibrium point is unstable.

This equilibrium represents the the extinction of the wrasse and the CoTS, while the coral survives.

4.1.4 Wrasse and Coral Extinction Equilibrium

The $E_3 = (0, 0, 1)$ is an equilibrium that always exist. The Jacobian evaluated at E_3 is provided by

$$J(E_3) = \begin{bmatrix} \delta_1 + \phi_1 & 0 & 0 \\ 0 & -\frac{\theta}{p} + \phi_2 & 0 \\ -\delta_2 & \frac{1}{p} & -\phi_3 \end{bmatrix},$$

which has the eigenvalues $\lambda_1 = \delta_1 + \phi_1$, $\lambda_2 = -\frac{\theta}{p} + \phi_2$, $\lambda_3 = -\phi_3$. This equilibrium is always unstable because the eigenvalue λ_1 will always be positive.

This equilibrium represents the survivorship of CoTS over time, while wrasse and coral go to extinction.

4.1.5 CoTS Extinction Equilibrium

The CoTS only extinction equilibrium, $E_4 = (1 + \beta, 1, 0)$, always exists. The Jacobian matrix evaluated at E_4 is given by:

$$J(E_4) = \begin{bmatrix} -\phi_1 & \phi_1\beta & (1 + \beta)\delta_1 \\ 0 & -\phi_2 & -\frac{\theta}{1+p} \\ 0 & 0 & \frac{1}{1+p} - (1 + \beta)\delta_2 + \phi_3 \end{bmatrix},$$

which has the eigenvalues $\lambda_1 = -\phi_1, \lambda_2 = -\phi_2$ and $\lambda_3 = \frac{1}{1+p} - (1 + \beta)\delta_2 + \phi_3$. Observe that λ_1 and λ_2 are always negative. Thus, the stability of this equilibrium depends on the sign of λ_3 . Then, the equilibrium E_4 is only unstable when $1 + \phi_3(p + 1) > (\beta + 1)(1 + p)\delta_2$, and otherwise is stable. Biologically, this equilibrium can be stable as the coral will live “happily ever after” without CoTS predation and the wrasse have other forms of food diet besides the CoTS.

4.1.6 Coral Only Exclusion Equilibrium

The existence of the coral only exclusion equilibrium $E_5 = \left(\frac{\phi_3(\delta_1 + \phi_1)}{\delta_1\delta_2 + \phi_1\phi_3}, 0, \frac{\phi_1(\phi_3 - \delta_2)}{\delta_1\delta_2 + \phi_1\phi_3} \right)$, is given by $\phi_3 > \delta_2$, otherwise this equilibrium does not exist. This condition means that the representation of intrinsic growth rate of the CoTS has to be greater than the detriment to the CoTS population from the presence of wrasse.

To analyze the stability of this equilibrium, we use estimated parameter values (see Section 8) on the Jacobian matrix 5.3, as analytical expression was difficult to achieve. We use the software *Wolfram Mathematica* 10.4 to calculate the eigenvalues of this matrix. The parameter values used for the analysis are as follows:

$$\phi_1 = 0.03, \phi_2 = 0.0259, \phi_3 = 0.26, \delta_1 = 5.5 \times 10^{-11}$$

$$\delta_2 = 0.15, \theta = 0.015873, \beta = 3.001025 \quad \text{and} \quad p = 0.765334.$$

Note that this parameter satisfied the existence conditions $\phi_3 = 0.26 > 0.15 = \delta_2$. Under this specific set of parameter values we obtained the following eigenvalues:

$$\lambda_1 = -0.11, \lambda_2 = -0.03 \text{ and } \lambda_3 = 0.02$$

Observe that λ_3 is positive, then the equilibrium is unstable. Biologically it means that wrasse and CoTS population might survive over time but in absence of the coral.

4.1.7 Wrasse Only Exclusion Equilibrium

Now we are going to analyze the wrasse only exclusion equilibrium - that is, when the coral and the starfish survive, but the wrasse becomes extinct, i.e $w = 0$. We will now provide a theorem that shows the existence of this equilibrium point. The mathematical analysis was too complicated for its analytical expression to be determined by inspection.

Theorem 1. *There is a unique wrasse only exclusion equilibrium $E_6 = (0, c_1^*, s_1^*)$ if $p\phi_2 > \theta$.*

Proof. Existence. Suppose that $p\phi_2 > \theta$. To calculate the wrasse only exclusion equilibria, we solve the system of equations given by

$$\phi_2(1 - c) - \frac{\theta s}{p + c} = 0, \quad (4.6a)$$

$$\text{and } \phi_3(1 - s) + \frac{c}{p + c} = 0. \quad (4.6b)$$

From Equation 4.6b we obtain

$$s(c) = \frac{(1 - c)\phi_2(c + p)}{\theta}. \quad (4.7)$$

Plugging Equation 4.7 in to Equation 4.6a, we obtain a third degree polynomial given by

$$f(c) = a_3c^3 + a_2c^2 + a_1c + a_0,$$

where $a_3 = \frac{\phi_2}{\theta}$, $a_2 = \frac{-\phi_2}{\theta} + \frac{2p\phi_2}{\theta}$, $a_1 = \left(1 - \frac{2p\phi_2}{\theta} + \frac{p^2\phi_2}{\theta} + \frac{1}{\phi_3}\right)$ and $a_0 = p\left(1 - \frac{p\phi_2}{\theta}\right)$. Since $f(c)$ is a polynomial, then it is continuous particularly in, $[0, 1]$. Notice that

$$f(0) = p\left(1 - \frac{p\phi_2}{\theta}\right).$$

Using the assumption that $p\phi_2 > \theta$ then

$$f(0) < 0,$$

on the other hand,

$$f(1) = p + \frac{1}{\phi_3} + 1 > 0.$$

By the Intermediate Value Theorem, there is a value $c_1^* \in (0, 1)$, such that $f(c_1^*) = 0$. Then there exists a positive real root c_1^* of $f(c)$.

Uniqueness. Through an initial computational analysis using *Mathematica 10.4* it was determined that two of these three roots were complex.

From our system we obtain that $s_1^*(c) = \left(\frac{(1 - c_1^*)\phi_2(c_1^* + p)}{\theta}\right)$

In conclusion, there is a unique equilibrium point - i.e, there is a unique wrasse only exclusion equilibrium $(0, c_1^*, s_1^*)$. ■

Notice that the condition $p\phi_2 > \theta$, represents the environment protection and the growth rate of the coral is greater than the destruction of the coral.

Now, we proceed to analyze the stability of this equilibrium, which is given by compu-

tational analysis. Using *Wolfram Mathematica 10.4*, we obtain the follow eigenvalues:

$$\lambda_1 = -0.281, \lambda_2 = 0.030, \text{ and } \lambda_3 = -0.002.$$

Since λ_2 is positive, then the equilibrium is unstable.

4.1.8 Coexistence Equilibria

The coexistence equilibrium point occurs when the wrasse, coral, and starfish survive along time. In the following, we provide a theorem that shows the existence of this equilibrium.

Theorem 2. *If $p\phi_2 > \theta$ and $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$, then there is at least one coexistence equilibrium point $E_7 = (w_2^*, c_2^*, s_2^*)$.*

Proof. To calculate the coexistence equilibrium point, suppose $p\phi_2 > \theta$ and $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$ and the following system of equations

$$\phi_1 \left(1 - \frac{w}{1 + \beta c} \right) + \delta_1 s = 0, \quad (4.8a)$$

$$\phi_2(1 - c) - \frac{\theta s}{p + c} = 0, \quad (4.8b)$$

$$\text{and } \phi_3(1 - s) + \frac{c}{p + c} - \delta_2 w = 0. \quad (4.8c)$$

Then we have

$$s(c) = \frac{(1 - c)\phi_2(c + p)}{\theta} \quad (4.9)$$

and

$$w(c) = \frac{\phi_3(c + p) \left(1 - \frac{(1-c)\phi_2(c+p)}{\theta} \right) + c}{\delta_2(c + p)}. \quad (4.10)$$

Therefore, plugging Eq. 4.9 and Eq. 4.10 into Eq. 4.8a, we obtain a polynomial function $f(c) = a_4c^4 + a_3c^3 + a_2c^2 + a_1c + a_0 = 0$, where

$$\begin{aligned}
a_4 &= \frac{\beta\delta_1\phi_2}{\theta\phi_1}, \\
a_3 &= -\frac{\beta\delta_1\phi_2}{\theta\phi_1} + \frac{\phi_3\phi_2}{\delta_2\theta} + \frac{\delta_1\phi_2}{\theta\phi_1} + \frac{2\beta\delta_1p\phi_2}{\theta\phi_1}, \\
a_2 &= -\beta - \frac{\delta_1\phi_2}{\theta\phi_1} - \frac{\phi_2\phi_3}{\delta_2\theta} + \frac{\beta\delta_1p^2\phi_2}{\theta\phi_1} - \frac{2\beta\delta_1p\phi_2}{\theta\phi_1} + \frac{2\delta_1p\phi_2}{\theta\phi_1} + \frac{2p\phi_2\phi_3}{\delta_2\theta}, \\
a_1 &= \frac{c\phi_3}{\delta_2} + \frac{c}{\delta_2} - \frac{\beta c\delta_1p^2\phi_2}{\theta\phi_1} + \frac{c\delta_1p^2\phi_2}{\theta\phi_1} + \frac{cp^2\phi_2\phi_3}{\delta_2\theta} - \beta cp - \frac{2c\delta_1p\phi_2}{\theta\phi_1} - \frac{2cp\phi_2\phi_3}{\delta_2\theta} - c, \\
a_0 &= -\frac{\delta_1p^2\phi_2}{\theta\phi_1} - \frac{p^2\phi_2\phi_3}{\delta_2\theta} + \frac{p\phi_3}{\delta_2} - p.
\end{aligned}$$

Using the assumptions that $p\phi_2 > \theta$ and $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$ we have:

$$f(0) = -\frac{\delta_1p^2\phi_2}{\theta\phi_1} + \frac{p\phi_3(1 - \frac{p\phi_2}{\theta})}{\delta_2} - p < 0,$$

and

$$f(1) = -(\beta+1)(p+1) + \frac{(p+1)\phi_3 + 1}{\delta_2} > 0.$$

Since $f(c)$ is continuous $\forall c \in [0, 1]$ and $f(0) < 0$ and $f(1) > 0$, then using the Intermediate Value Theorem (Bolzano's Theorem), we conclude that there is a positive real root, denoted c^* , such that $f(c^*) = 0$. Therefore, $s^* = (\frac{(1-c^*)\phi_2(c^*+p)}{\theta})$ and $w^* = \frac{\phi_3(c^*+p)(1 - \frac{(1-c^*)\phi_2(c^*+p)}{\theta}) + c^*}{\delta_2(c^*+p)}$.

Thus, a coexistence equilibria point (w^*, c^*, s^*) exists. ■

Observe that if $E_4 = (1 + \beta, 1, 0)$ is unstable then we have $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$, and that is one of the conditions to guarantee the existence of the equilibrium $E_7 = (w_2^*, c_2^*, s_2^*)$. So if the equilibrium E_4 is stable, we can not guarantee the existence of E_7 .

Now, we are going to numerically analyze the stability. Using *Wolfram Mathematica 10.4*, we find the follow eigenvalues:

$$\lambda_1 = -0.27, \lambda_2 = -0.05 \text{ and } \lambda_3 = -0.01$$

Observe that all the eigenvalues are negative, so the equilibrium is stable. This stability implies that this coexistence is possible. All three species can persist together for a prolonged period of time, just as they have in the reefs of Raja Ampat.

The conditions for existence and stability of each equilibrium are summarized in

the following table (Table 3).

| Equilibrium | Existence | Stability |
|--|---|---|
| $E_0 = (0, 0, 0)$ | always | unstable |
| $E_1 = (1, 0, 0)$ | always | unstable |
| $E_2 = (0, 1, 0)$ | always | unstable |
| $E_3 = (0, 0, 1)$ | always | unstable |
| $E_4 = (1 + \beta, 1, 0)$ | always | if $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$ then is unstable |
| $E_5 = \left(\frac{\phi_3(\delta_1 + \phi_1)}{\delta_1\delta_2 + \phi_1\phi_3}, 0, \frac{\phi_1(\phi_3 - \delta_2)}{\delta_1\delta_2 + \phi_1\phi_3} \right)$ | $\phi_3 > \delta_2$ | unstable (computational) |
| $E_6 = (0, c_1^*, s_1^*)$ | $p\phi_2 > \theta$ | unstable (computational) |
| $E_7 = (w_2^*, c_2^*, s_2^*)$ | $\phi_3 > \delta_2$ and $1 + \phi_3(p+1) > (\beta+1)(1+p)\delta_2$ | locally stable (computational) |

Table 3: Summary of conditions for existence and stability of System 4.3

5 Model with Constant Effort Harvesting

In this section, we analyze the model with constant effort wrasse harvesting. We assume that the fishers make the same effort at all times to catch wrasse, making the harvest directly proportional to wrasse biomass. Some portion of this harvest is carried out using cyanide and blast - both of which cause coral mortality. As harvesting increases, the amount of cyanide pumped and blast thrown into the sea will also increase, resulting in greater coral mortality. As wrasse population directly benefits from increased coral population, we can model destruction as a constant effort “harvest” of coral - the more coral present, the more will exit the system via destruction from cyanide and blast.

We now proceed to analyze Model 3.2, for which $H(t) = H$ and $D(t) = D$, which

is given by the following equations:

$$\dot{W} = W \left[r_1 \left(1 - \frac{W}{K_1 + bC} \right) + \alpha_1 S \right] - HW, \quad (5.1a)$$

$$\dot{C} = C \left[r_2 \left(1 - \frac{C}{K_2} \right) - \frac{\gamma_1 S}{C + q} \right] - DC, \quad (5.1b)$$

$$\text{and } \dot{S} = S \left[r_3 \left(1 - \frac{S}{K_3} \right) - \alpha_2 W + \frac{\gamma_2 C}{C + q} \right]. \quad (5.1c)$$

Our new System 5.1 is a more general case of System 4.1 and can be reduced to it by considering $H = 0, D = 0$. Therefore equilibria, existence conditions and results associated to Model 3.2 holds to those of Model 5.1 in the previous section (Section 4), when $H = 0, D = 0$.

We non-dimensionalize System 5.1 as before to obtain the following system of equations:

$$\frac{dw}{d\tau} = w \left[\phi_1 \left(1 - \frac{w}{1 + \beta c} \right) + \delta_1 s \right] - hw, \quad (5.2a)$$

$$\frac{dc}{d\tau} = c \left[\phi_2 (1 - c) - \frac{\theta s}{p + c} \right] - dc, \quad (5.2b)$$

$$\frac{ds}{d\tau} = s \left[\phi_3 (1 - s) + \frac{c}{p + c} - \delta_2 w \right], \quad (5.2c)$$

where $\phi_i = \frac{r_i}{\gamma_2}$ for $i = 1, 2, 3$; $\beta = \frac{k_2 b}{k_1}$; $p = \frac{q}{k_2}$; $\delta_1 = \frac{k_3 \alpha_1}{\gamma_2}$; $\delta_2 = \frac{\alpha_2 k_1}{\gamma_2}$; $\theta = \frac{\gamma_1 k_3}{\gamma_2 k_2}$; and

$$h = \frac{H}{\gamma_2}, d = \frac{D}{\gamma_2}.$$

We proceed to analyze the system, first calculating the equilibria and their existence, then establishing their stability. In some cases, we find that the equilibria are always existing, and in others we provide conditions for existence. The stability analysis is carried out “directly” or using numerical computational analysis.

The system has at least eight possible equilibria, denoted by $E_i = (w^*, c^*, s^*)$ for $i = 0, \dots, 7$:

$$\begin{aligned}
E_0 &= (0, 0, 0), & E_4 &= \left(\frac{(\phi_1 - h)(\beta(\phi_2 - d) + \phi_2)}{\phi_1 \phi_2}, \frac{\phi_2 - d}{\phi_2}, 0 \right), \\
E_1 &= \left(\frac{\phi_1 - h}{\phi_1}, 0, 0 \right), & E_5 &= \left(\frac{\phi_3(\delta_1 + \phi_1 - h)}{\delta_1 \delta_2 + \phi_1 \phi_3}, 0, \frac{\delta_2(h - \phi_1) + \phi_1 \phi_3}{\delta_1 \delta_2 + \phi_1 \phi_3} \right), \\
E_2 &= \left(0, \frac{\phi_2 - d}{\phi_2}, 0 \right), & E_6 &= (0, c_1^*, s_1^*), \\
E_3 &= (0, 0, 1), & \text{and} & E_7 = (w_2^*, c_2^*, s_2^*).
\end{aligned}$$

Observe that the equilibrium points E_0, E_3 always exist. The existence of equilibria E_1, E_2, E_4, E_5 , on the other hand, are conditional. In the cases of equilibria E_6 and E_7 , we provide a proof of existence.

To analyze the stabilities of E_0, E_1, E_2, E_3, E_4 , we calculate the Jacobian matrix of the rescaled System 5.4b, and obtain the follow matrix:

$$J(w, c, s) := \begin{bmatrix} s\delta_1 + \phi_1 - h - 2\frac{w\phi_1}{c\beta+1} & \frac{w^2\beta\phi_1}{(c\beta+1)^2} & w\delta_1 \\ 0 & \phi_2 - d - 2\phi_2c - \frac{\theta sp}{(p+c)^2} & -\frac{c\theta}{c+p} \\ -s\delta_2 & \frac{sp}{(p+c)^2} & \frac{c}{c+p} - 2\phi_3s + \phi_3 \end{bmatrix}. \quad (5.3)$$

We now present a detailed analysis of the existence and stability of all the equilibria for this system. Notice that all eigenvalues and conditions for existence reduce to those presented in Section 4 for the model without harvesting or destruction (when $h = 0, d = 0$).

5.1 Extinction Equilibrium

The trivial equilibrium $E_0 = (0, 0, 0)$ always exists. The Jacobian Matrix 5.3 evaluated at the trivial equilibrium is provided by

$$J(E_0) = \begin{bmatrix} \phi_1 - h & 0 & 0 \\ 0 & \phi_2 - d & 0 \\ 0 & 0 & \phi_3 \end{bmatrix}.$$

The eigenvalues are $\lambda_1 = \phi_1 - h$, $\lambda_2 = \phi_2 - d$ and $\lambda_3 = \phi_3$. Since λ_3 is positive, this equilibrium is unstable.

5.2 Coral and Starfish Exclusion Equilibrium

The equilibrium $E_1 = \left(\frac{\phi_1 - h}{\phi_1}, 0, 0\right)$ exists if $\phi_1 > h$, i.e. $r_1 > H$ in terms of the original parameters. That is, E_1 exists if the wrasse growth rate is larger than the rate at which it is harvested. The coral and the starfish disappear and only the wrasse survive.

The Jacobian Matrix 5.3 evaluated at E_1 is given by:

$$J(E_1) = \begin{bmatrix} h - \phi_1 & \frac{\beta(h - \phi_1)^2}{\phi_1} & \delta_1 \left(1 - \frac{h}{\phi_1}\right) \\ 0 & \phi_2 - d & 0 \\ 0 & 0 & \delta_2 \left(\frac{h}{\phi_1} - 1\right) + \phi_3 \end{bmatrix},$$

with eigenvalues

$$\lambda_1 = h - \phi_1, \lambda_2 = \phi_2 - d, \text{ and } \lambda_3 = \delta_2 \left(\frac{h}{\phi_1} - 1\right) + \phi_3.$$

Observe that if $\phi_2 > d$, then λ_2 is positive. Therefore, the equilibrium is unstable. Biologically, this means that if the growth rate of the coral is greater than the rate at which it is destroyed by IUU fishing, then the coral population will not go extinct. The population rebounds, and the system moves away from this equilibrium. However, if $d > \phi_2$ and $\phi_3 < \delta_2(\frac{h}{\phi_1} - 1)$, then E_1 can be stable.

5.3 Wrasse and Starfish Exclusion Equilibrium

Equilibrium $E_2 = \left(0, \frac{\phi_2 - d}{\phi_2}, 0\right)$ exists if $\phi_2 > d$ - i.e. $r_2 > D$, in terms of the original parameters. This means that the rate of coral growth is higher than the rate at which it is destroyed by IUU fishing. The Jacobian Matrix 5.3 at this equilibrium is

$$J(E_2) = \begin{bmatrix} \phi_1 - h & 0 & 0 \\ 0 & d - \phi_2 & \frac{\Theta(\phi_2 - d)}{d - (p+1)\phi_2} \\ 0 & 0 & \frac{d - \phi_2}{d - (p+1)\phi_2} + \phi_3 \end{bmatrix}.$$

The eigenvalues are

$$\lambda_1 = \phi_1 - h, \lambda_2 = d - \phi_2, \text{ and } \lambda_3 = \frac{d - \phi_2}{d - (p+1)\phi_2} + \phi_3.$$

This equilibrium exists if $\phi_1 > h$, that is the growth rate of the wrasse is great than the rate at which it is destroyed by IUU fishing. This implies that $\lambda_1 > 0$ then the

equilibrium is unstable.

5.4 Wrasse and Coral Extinction Equilibrium

The wrasse and coral extinction equilibrium, $E_3 = (0, 0, 1)$, always exists. The Jacobian Matrix 5.3 evaluated at E_3 is given by

$$J(E_3) = \begin{bmatrix} \delta_1 + \phi_1 - h & 0 & 0 \\ 0 & \phi_2 - \frac{\theta}{p} - d & 0 \\ -\delta_2 & \frac{1}{p} & -\phi_3 \end{bmatrix},$$

which has eigenvalues $\lambda_1 = \delta_1 + \phi_1 - h$, $\lambda_2 = \phi_2 - \frac{\theta}{p} - d$ and $\lambda_3 = -\phi_3$.

The equilibrium is unstable if $\phi_1 + \delta_1 > h$. This means that the rate at which wrasse exit the system via harvest is less than the overall growth of the wrasse population. However if $\delta_1 + \phi_1 < h$ and $p\phi_2 > \theta + pd$ then E_3 can be stable.

5.5 Starfish Only Exclusion Equilibrium

The starfish only exclusion equilibrium $E_4 = \left(\frac{(\phi_1 - h)(\beta(\phi_2 - d) + \phi_2)}{\phi_1 \phi_2}, \frac{\phi_2 - d}{\phi_2}, 0 \right)$ exists if $\phi_1 > h$ and $\phi_2 > d$. The Jacobian matrix 5.3 evaluated at E_4 is

$$J(E_4) = \begin{bmatrix} h - \phi_1 & \frac{\beta(h - \phi_1)^2}{\phi_1} & \frac{\delta_1(\phi_1 - h)((\beta + 1)\phi_2 - d\beta)}{\phi_1 \phi_2} \\ 0 & d - \phi_2 & \frac{\Theta(\phi_2 - d)}{d - (p + 1)\phi_2} \\ 0 & 0 & \frac{d - \phi_2}{d - (p + 1)\phi_2} + \frac{\delta_2(h - \phi_1)((\beta + 1)\phi_2 - d\beta)}{\phi_1 \phi_2} + \phi_3 \end{bmatrix}.$$

The eigenvalues of $J(E_4)$ are

$$\lambda_1 = h - \phi_1, \lambda_2 = d - \phi_2$$

and $\lambda_3 = \frac{d - \phi_2}{d - (p + 1)\phi_2} + \frac{\delta_2(h - \phi_1)((\beta + 1)\phi_2 - d\beta)}{\phi_1 \phi_2} + \phi_3.$

Observe that λ_1 and λ_2 are negative for the conditions given for the existence. The stability of this equilibrium, then, depends on the third eigenvalue λ_3 .

If $\phi_3 + \frac{\phi_2 - d}{\phi_2 - d + p} > \frac{\delta_2(\phi_1 - h)(\beta(\phi_2 - d) + \phi_2)}{\phi_1 \phi_2}$, then the equilibrium is unstable,

otherwise the equilibrium can be stable.

5.6 Coral Only Exclusion Equilibrium

The equilibrium $E_5 = \left(\frac{\phi_3(\delta_1 + \phi_1 - h)}{\delta_1\delta_2 + \phi_1\phi_3}, 0, \frac{\delta_2(h - \phi_1) + \phi_1\phi_3}{\delta_1\delta_2 + \phi_1\phi_3} \right)$ only exists when $0 < h - \phi_1 < \delta_1$. This means that the intrinsic growth rate of the CoTS has to be greater than the detriment to the CoTS population from the wrasse being in the environment for this equilibrium to exist biologically.

However, due to the complexity of the analytic eigenvalues, we proceed to calculate the eigenvalues numerically with a set of parameters that satisfy the conditions of existence (see Section 8), which are

$$\begin{aligned} \phi_1 &= 0.03, \phi_2 = 0.0259, \phi_3 = 0.26, \delta_1 = 5.5 \times 10^{-11}, \delta_2 = 0.15, \\ \theta &= 0.015873, \beta = 3.001025, p = 0.66276, h = 0.03, d = 0.02. \end{aligned}$$

Through the use of *Wolfram Mathematica 10.4*, we found the eigenvalues of this equilibrium numerically, they are

$$\lambda_1 = -0.15, \lambda_2 = -0.02 \quad \text{and} \quad \lambda_3 = 0.11$$

Observe that λ_3 is positive, then the equilibrium is unstable.

5.7 Wrasse Only Exclusion Equilibrium

We analyze the equilibrium in which no wrasse population biomass are present - but CoTS and coral exist. Coral are able to survive without the trophic cascade provided by wrasse; and CoTS are free from predation by wrasse.

Theorem 3. *There is a unique wrasse only exclusion equilibrium $(0, c_1^*, s_1^*)$ if $p\phi_2 > \theta + dp$.*

Proof. Existence. To calculate the wrasse only exclusion equilibrium, we suppose $p\phi_2 > \theta + dp$ and solve the follow system of equations given by

$$\phi_2(1 - c) - \frac{\theta s}{p + c} - dc = 0, \tag{5.4a}$$

$$\phi_3(1 - s) + \frac{c}{p + c} = 0. \tag{5.4b}$$

From Equation 5.4a, we have

$$s(c) = \frac{(1 - c)\phi_2(c + p)}{\theta} - \frac{d(c + p)}{\theta}. \tag{5.5}$$

Plug Equation 5.5 in Equation 5.4b, then we obtain a third degree polynomial

$$f(c) = a_3c^3 + a_2c^2 + a_1c + a_0,$$

where $a_3 = \frac{\phi_2}{\theta}$, $a_2 = \frac{d}{\theta} - \frac{\phi_2}{\theta} + \frac{2p\phi_2}{\theta}$, $a_1 = 1 - \frac{2p\phi_2}{\theta} + \frac{p^2\phi_2}{\theta} + \frac{1}{\phi_3} + \frac{2dp}{\theta}$, $a_0 = p - \frac{p^2\phi_2}{\theta} + \frac{dp^2}{\theta}$.

We want to proof the existence of c_1^* that satisfies $f(c_1^*) = 0$.

Since $f(c)$ is a polynomial, then $f(c)$ is continuous in $[0, 1]$. Using the assumption that $p\phi_2 > \theta + dp$ then

$$f(0) = \frac{p(dp + \theta - p\phi_2)}{\theta} < 0$$

and

$$f(1) = p + \frac{1}{\phi_3} + 1 + \frac{d}{\theta} + \frac{2dp}{\theta} + \frac{dp^2}{\theta} > 0,$$

by the Intermediate Value Theorem (Bolzano's Theorem), there is a $c_1^* \in (0, 1)$ such that $f(c_1^*) = 0$.

Uniqueness. Through an initial computational analysis using *Wolfram Mathematica 10.4*, it was determined that two of these three roots are complex.

From our system we obtain that

$$s_1 * (c_1^*) = \frac{(1 - c_1^*)\phi_2(c_1^* + p)}{\theta} - \frac{d(c_1^* + p)}{c_1^* \theta}$$

In conclusion, there is a unique equilibrium point i.e, there is a wrasse Only Exclusion Equilibrium $(0, c_1^*, s_1^*)$. ■

The stability of this equilibrium is given by calculating the eigenvalues of Matrix (5.3) at E_7 . They are given by

$$\lambda_1 = -0.270, \lambda_2 = 0.022 \text{ and } \lambda_3 = -0.001.$$

Notice that $\lambda_2 > 0$. Thus, E_7 is unstable.

5.8 Coexistence Equilibrium

We next analyze the equilibrium at which all three populations persist over time and none are driven to extinction. The populations reach a certain biomass at which they remain. Because this equilibrium point is too complicated for its analytical expression to be determined by inspection, we prove existence with the following theorem:

Theorem 4. *Assume that*

$$1 + \frac{p\phi_2\phi_3}{\delta_2\theta} + \frac{p\phi_2\delta_1}{\theta} > \frac{\phi_3}{\delta_2} + \frac{pd}{\theta} \left(\frac{\delta_1}{\phi_1} + \phi_3 \right) + \frac{h}{\phi_1} \quad (5.6)$$

and

$$(1+p) \frac{\phi_1\phi_3}{\delta_2} + \frac{\phi_1}{\delta_2} + (1+p)(1+\beta) \left[\frac{(1+p)\delta_1d}{\theta} + h \right] + (1+p^2) \frac{\phi_1\phi_3d}{\delta_2\theta} > \phi_1(1+p)(1+\beta) \quad (5.7)$$

then there is at least one coexistence equilibrium point $E_7 = (w_2^*, c_2^*, s_2^*)$.

Proof. We assume Expressions 5.6 and 5.7 and solve the following system of equations:

$$\phi_1 \left(1 - \frac{w}{1+\beta c} \right) + \delta_1 s = 0, \quad (5.8a)$$

$$\phi_2(1-c) - \frac{\theta s}{p+c} = 0, \quad (5.8b)$$

$$\text{and } \phi_3(1-s) + \frac{c}{p+c} - \delta_2 w = 0. \quad (5.8c)$$

To calculate the coexistence equilibria point we solve the equations in terms of c ,

$$s(c) = \frac{(c+p)((1-c)\phi_2 - d)}{\theta} \quad (5.9)$$

and

$$w(c) = \frac{\phi_3(c+p) \left(1 - \frac{(c+p)((1-c)\phi_2 - d)}{\theta} \right) + c}{\delta_2(c+p)}. \quad (5.10)$$

Therefore, plugging Eqs. 5.9 and Eq. 5.10 into Equation 5.8a, we obtain a polynomial function

$$f(c) = a_4 c^4 + a_3 c^3 + a_2 c^2 + a_1 c + a_0 = 0,$$

where

$$\begin{aligned}
a_4 &= \frac{\beta\delta_1\phi_2}{\theta}, \\
a_3 &= -\frac{\beta\delta_1\phi_2}{\theta} + \frac{\beta d\delta_1}{\theta} + \frac{\delta_1\phi_2}{\theta} + \frac{\phi_1\phi_2\phi_3}{\delta_2\theta} + \frac{2\beta\delta_1 p\phi_2}{\theta}, \\
a_2 &= -\beta\phi_1 + \frac{d\phi_1\phi_3}{\delta_2\theta} + \frac{d\delta_1}{\theta} - \frac{\delta_1\phi_2}{\theta} - \frac{\phi_1\phi_2\phi_3}{\delta_2\theta} + \\
&\quad \frac{2\beta d\delta_1 p}{\theta} + \beta h + \frac{\beta\delta_1 p^2\phi_2}{\theta} - \frac{2\beta\delta_1 p\phi_2}{\theta} + \frac{2\delta_1 p\phi_2}{\theta} + \frac{2p\phi_1\phi_2\phi_3}{\delta_2\theta} \\
a_1 &= \frac{\beta cd\delta_1 p^2}{\Theta} + \frac{2cdp\phi_1\phi_3}{\delta_2\Theta} + \frac{2cd\delta_1 p}{\Theta} + \frac{c\phi_1}{\delta_2} + \frac{c\phi_1\phi_3}{\delta_2} + \beta chp + ch - \\
&\quad \frac{\beta c\delta_1 p^2\phi_2}{\Theta} + \frac{c\delta_1 p^2\phi_2}{\Theta} + \frac{cp^2\phi_1\phi_2\phi_3}{\delta_2\Theta} - \beta cp\phi_1 - \frac{2c\delta_1 p\phi_2}{\Theta} - \frac{2cp\phi_1\phi_2\phi_3}{\delta_2\Theta} - c\phi_1 \\
a_0 &= \frac{dp^2\phi_1\phi_3}{\delta_2\Theta} + \frac{d\delta_1 p^2}{\Theta} + hp - \frac{\delta_1 p^2\phi_2}{\Theta} - \frac{p^2\phi_1\phi_2\phi_3}{\delta_2\Theta} + \frac{p\phi_1\phi_3}{\delta_2} - p\phi_1.
\end{aligned}$$

Using Equations 5.6 and 5.7 we have:

$$f(0) = p\phi_1 \left[\frac{\phi_3}{\delta_2} + \frac{pd}{\theta} \left(\frac{\delta_1}{\phi_1} + \phi_3 \right) + \frac{h}{\phi_1} - 1 - \frac{p\delta_1\phi_2}{\theta} - \frac{p\phi_2\phi_3}{\delta_2\theta} \right] < 0,$$

and

$$f(1) = (1+p)\frac{\phi_1\phi_3}{\delta_2} + \frac{\phi_1}{\delta_2} + (1+p)(1+\beta) \left[(1+p)\frac{\delta_1 d}{\theta} + h \right] + (1+p^2)\frac{\phi_1\phi_3 d}{\delta_2\theta} - \phi_1(1+p)(1+\beta) > 0.$$

Since $f(c)$ is continuous $\forall c \in [0, 1]$ and $f(0) < 0$ and $f(1) > 0$ using Intermediate Value Theorem (Bolzano's Theorem), we conclude that there is a real positive root, denoted c_2^* , such a $f(c_2^*) = 0$ therefore

$$s_2^* = \frac{(c_2^* + p)((1 - c_2^*)\phi_2 - d)}{\theta}$$

and

$$w_2^* = \frac{\phi_3(c_2^* + p) \left(1 - \frac{(1 - c_2^*)\phi_2(c_2^* + p)}{\theta} \right) + c_2^*}{\delta_2(c_2^* + p)}.$$

Thus, a coexistence equilibrium point (w_2^*, c_2^*, s_2^*) exists. ■

As in other cases, the stability of the equilibria will be calculated using computational analysis. The eigenvalues of this equilibrium are:

$$\lambda_1 = -0.267, \lambda_2 = -0.027 \quad \text{and} \quad \lambda_3 = -0.006.$$

All of the eigenvalues are negative, hence the coexistence equilibrium is locally stable.

The results are summarized in the following table.

| Equilibria | Existence | Stability |
|--|---|--|
| $E_0 = (0, 0, 0)$ | Always | Unstable |
| $E_1 = (\frac{\phi_1 - h}{\phi_1}, 0, 0)$ | If $\phi_1 > h$ | If $\phi_2 > d$ then is unstable |
| $E_2 = (0, \frac{\phi_2 - d}{\phi_2}, 0)$ | If $\phi_2 > d$ | Unstable |
| $E_3 = (0, 0, 1)$ | Always | If $\phi_1 + \delta_1 > h$ then is unstable |
| $E_4 = \left(\frac{(\phi_1 - h)(\beta(\phi_2 - d) + \phi_2)}{\phi_1 \phi_2}, \frac{\phi_2 - d}{\phi_2}, 0 \right)$ | If $\phi_1 > h$ and $\phi_2 > d$ | If $\phi_3 + \frac{d - \phi_2}{d - (p+1)\phi_2} > \frac{\delta_2(\phi_1 - h)(\beta(\phi_2 - d) + \phi_2)}{\phi_1 \phi_2}$ Then it is unstable |
| $E_5 = \left(\frac{\phi_3(\delta_1 + \phi_1 - h)}{\delta_1 \delta_2 + \phi_1 \phi_3}, 0, \frac{\delta_2(h - \phi_1) + \phi_1 \phi_3}{\delta_1 \delta_2 + \phi_1 \phi_3} \right)$ | If $0 < h - \phi_1 < \delta_1$ | Unstable (computational) |
| $E_6 = (0, c_1^*, s_1^*)$ | If $p\phi_2 > \theta + dp$ | Unstable (computational) |
| $E_7 = (w_2^*, c_2^*, s_2^*)$ | $\Delta_1 > \Delta_2$ and $\Delta_3 < \Delta_4$ | Locally Stable (computational) |
| Where: $\Delta_1 = 1 + \frac{p\phi_2\phi_3}{\delta_2\theta} + \frac{p\phi_2\delta_1}{\theta}$, $\Delta_2 = \frac{\phi_3}{\delta_2} + \frac{pd}{\theta} \left(\frac{\delta_1}{\phi_1} + \phi_3 \right) + \frac{h}{\phi_1}$, $\Delta_3 = \phi_1(1 + p)(1 + \beta)$ and, $\Delta_4 = (1 + p)\frac{\phi_1\phi_3}{\delta_2} + \frac{\phi_1}{\delta_2} + (1 + p)(1 + \beta) \left[\frac{(1+p)\delta_1 d}{\theta} + h \right] + (1 + p^2)\frac{\phi_1\phi_3 d}{\delta_2\theta}$ | | |

Table 4: Summary of conditions for existence and stability of system (5.1)

6 Parameter Estimation

In this section, we show the parameter values we estimated for the simulations of our model. Some parameter values were estimated from literature and others were based on of assumptions. We will now proceed to explain how we obtained each parameter value.

Wrasse carrying capacity, K_1 :

Krista S Graham [13], provided an overview of general information about the Humphead wrasse. We estimated the natural carrying capacity of the wrasse within 1 km² to be one third of its maximum observed carrying capacity in the presence of coral which is 2000 wrasse per km². From biographical studies on the humphead wrasse [23] we estimated the wrasse's average mass to be 181 kg. Thus we computed the carrying capacity of the wrasse to be $\frac{2000}{3}$ times 181 = 120667 kg/km².

Coral carrying capacity, K_2 :

In our work we consider an area of 1 km² and from several studies [25] conducted on growth of different species of hard coral it was found that coral has a mass of 5mg/cm², from which we calculate 1 km² of coral to be 50,000 kg/km² which we take to be the carrying capacity of the coral.

CoTS carrying capacity, K_3 :

De'ath et al [9], conducted a study on factors within an ecosystem that affect CoTS behavior. The work was conducted on the Great Barrier Reef, where it suggests that CoTS are also able to feed on organisms other than hard coral such as soft corals and algae [5]. Based on this study, we estimated 550 kg/km² to be the natural carrying capacity of the CoTS.

Conversion rate of biomass from CoTS to wrasse, α_1 :

Randall [22] led a study on the digestive tract of the humphead wrasse and concluded that CoTS class, Asteroidea, only made up about 3.4% of the surveyed wrasses' digestive tracts. Judging from the size of the wrasse relative to the CoTS and considering the information found in this study, we estimated the conversion rate of biomass from CoTS to wrasse to be about 5×10^{-14} kg/km² a year for each CoTS eaten by a wrasse per year.

Predations rate of biomass on CoTS from wrasse, α_2 :

Graham's work [13] also showed the Humphead wrasse being one of the few predators that is willing and able to eat toxic animals such as the CoTS. From this report, we estimated that the Humphead wrasse must predate on the CoTS at a rate that can keep the population in check and in coexistence with the rest of the ecosystem. Based on this information and simulation trials, we estimated a yearly loss of CoTS biomass due to wrasse predation of 6.21545×10^{-9} kg/km².

Intrinsic growth rate of the wrasse, r_1 :

Graham [13] observed that it takes 5-7 years for a wrasse to reach sexual maturity and that wrasse have a tendency to spawn throughout the year. Also, in a study on wrasse spawning [8], Colin notes that predation on wrasse eggs is uncommon in the ecosystem. From these, we estimated the intrinsic growth rate of the wrasse biomass to be 1.5×10^{-4} kg/km² per year.

Intrinsic growth rate of the coral, r_2 :

Buddmeier et al. [7] studied many different species of coral and their growth

rates. Since we are interested in Sclerectinia coral which is made up of many different species of hard coral, we estimated, based on simulations, and the paper that the intrinsic growth rate of the coral biomass to be 0.000129 kg/km^2 per year.

Intrinsic growth rate of the CoTS, r_3 :

Fabricius et al. [11] notes that the CoTS takes two years to reach adulthood and estimates survival rates of the CoTS for the first seven years of its life. From this study, we estimated the intrinsic growth rate of the CoTS to be $1.3 \times 10^{-3} \text{ kg/km}^2$ per year.

Predation rate of coral from CoTS, γ_1 :

Keesing's PhD thesis [16] focuses on the eating rates of CoTS. Based on his study, we assume that the CoTS within Raja Ampat to average at 25cm in diameter. From the size of the CoTS we estimated the loss of coral biomass yearly from each CoTS to be $7.215 \times 10^{-3} \text{ kg/km}^2$.

Conversion rate of biomass from coral to CoTS, γ_2 :

From Keesing's thesis [16], we also estimated that the conversion rate from coral to CoTS biomass to be 0.005 kg/km^2 for each year for each CoTS in the environment.

Conversion factor from coral to wrasse biomass carrying capacity, b :

The value of b was based on general studies of the characteristics and the fact that wrasse reside within coral reefs observed and recorded by Graham, [13]. The information in the report influenced our estimate but the estimate was not taken directly from the report. We assumed that the wrasse's carrying capacity should be tripled in the presence of coral that is at carrying capacity. In the non-dimensionalized model, this translates to $\beta = 3$. So, we took $\frac{K_1 b}{K_2} \approx 3$ and calculated b to be 7.242494 based on our values from K_1 and K_2 .

CoTS mid-saturation threshold for predation on coral, q :

Calculated from possible estimated steady states of the ecosystem and the estimated eating rate of the CoTS which we take to be 10 m^2 a year [20] We took the estimated mass of 0.5 kg per year and from this we then set the $\frac{C\gamma_2 S}{C+q} \approx 0.5$ and used varying estimates of possible steady states to calculate q . One of the cases we used was $S = 14000$, $C = 14000$ and calculated that a $q = 33138 \text{ kg/km}^2 \approx 0.5$.

Function of harvest on the wrasse, $H(t)$:

The rate at which wrasse are harvested from the area will be varied in between a range of $(0, 0.04)$. This range was estimated based on simulations and we hope to include, in our future work, calculations of maximum sustainable yield so that we may have a more accurate maximum value for harvest.

Function of destruction to the coral, $D(t)$:

The rate at which coral is destroyed by harmful fishing practices in the area

will be varied in between a range of $(0, 0.04)$. This range was estimated based on simulations and we hope, in our future work, to calculate the maximum sustainable yield for coral in order to have a more accurate maximum value for destruction.

Table 5: Model Parameter Values

| Parameter | Definition | Values | References |
|------------|--|--------------------------|------------|
| K_1 | Carrying capacity of wrasse | 120667 | [13]; [23] |
| K_2 | Carrying capacity of coral | 50000 | [25] |
| K_3 | Carrying capacity of CoTS | 550 | [9] |
| α_1 | Conversion rate of biomass from CoTS to wrasse | 5×10^{-17} | [22] |
| α_2 | Predation rate of CoTS from wrasse | 6.21545×10^{-9} | [13] |
| r_1 | Intrinsic growth rate of wrasse | 0.00015 | [8]; [13] |
| γ_1 | Predation rate from CoTS on coral | 0.007215 | [16] |
| γ_2 | Conversion rate of Biomass from coral to CoTS | 0.005 | [16] |
| b | Conversion factor from coral to wrasse carrying capacity | 7.242494 | Estimated |
| q | CoTS mid-saturation threshold from coral consumption | 33138 | Estimated |
| H | Function of wrasse harvest | $(0, 0.04)$ | Estimated |
| D | Function of coral destruction | $(0, 0.04)$ | Estimated |

7 Simulations

In this section, we will numerically simulate our dimensionless model for constant effort harvesting, using *MATLAB's ODE* solver *ode45*. We will assume the initial conditions ($w(0) = 0.1, c(0) = 0.28, s(0) = 0.02$) for our special case where there is no harvest or destruction ($h = 0$ and $d = 0$ in Figure 1). All the simulations presented in this section were done with the values found in Table 5. Furthermore, the focus

of our simulations are the destruction and harvest parameters, d and h respectively, because our methods of intervention include minimizing human intervention.

First, we will consider a special case, which is where there are no outside disturbances, that is no harvesting nor destruction ($h = 0$ and $d = 0$). The case is chosen to provide insight on the behavior of the system in the absence of human intervention. We then consider the effects of constant effort harvesting, simulated by the harvesting (h) and destruction (d) factors and observe how combinations of these parameter values affects our ecosystem model 4.4.

Each simulation consists of three plots, which represent each species' biomass (in $\frac{kg}{km^2}$) in relation to their respective carrying capacities, which are independent from one another. We numerically simulate the change in each species' biomass in years. It is our assumption that growth enhancing organisms; such as the coral, are only able to grow to its natural carrying capacity. Should an organism have a biomass above 1, it is only because the presence of another organism, i.e, the coral, has allowed it to grow above its natural carrying capacity. One such case is the Humphead wrasse, which, in the absence of coral, has a very limited carrying capacity. The actual number of individuals at a year t can be obtained by multiplying the value of each species at year t by their own carrying capacity and dividing by the averaged mass respective to each species (see discussion in Parameter Estimation).

7.1 Harvest and Destruction Exclusion Simulations

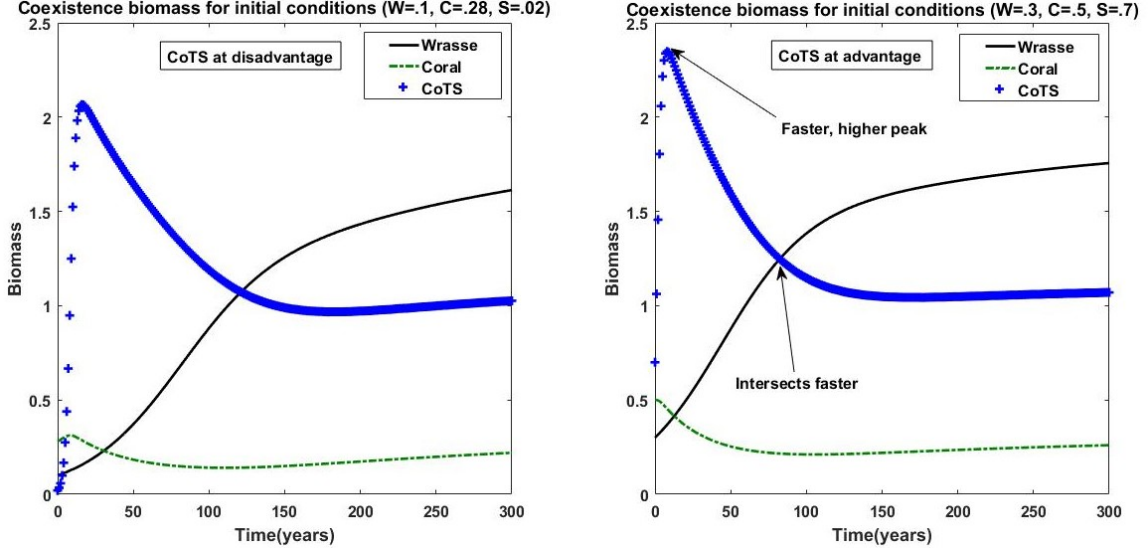


Figure 3: Coexistence simulation in the absence of harvest and destruction with varying initial conditions ($W(0) = 0.1, C(0) = 0.28, S(0) = 0.02$)(a) and ($W(0) = 0.3, C(0) = 0.5, S(0) = 0.7$)(b).

Figure 1 shows that the three species can live in coexistence with each other. We first simulated the system with initial conditions extrapolated from data provided by Table 5. We then varied them to see if we would get the same result. The plot in Figure 3 was obtained with initial conditions of $w(0) = 0.1, c(0) = 0.28$, and $s(0) = 0.02$. We then altered the initial conditions to be unfavorable to the coral, where we start with $w(0) = 0.3, c(0) = 0.5$ and $s(0) = 0.7$ to study how influential initial conditions would be on the outcome of the simulation. Note that, on Figure 1(a), the CoTS biomass begins a sharp increase for the first 2 decades. After which, it steeply declines until it gradually stabilizes at around the 125 year mark. The coral biomass, on the other hand, only appears to grow for the first few years after which it gradually decreases, apparently stabilizing and slowly recovering at the 100 year mark. Now, observe that the wrasse biomass appears to grow along with the CoTS biomass, where, as one decreases, the other grows. It is also worth noticing that the wrasse and CoTS biomass begin to stabilize after year 150. The plot allows us to observe the typical behavior of our system. The same behaviors apply to Figure 3(b), where the only difference appears to be that the system progresses slightly faster toward equilibrium. Hence, we conclude that the system always reaches equilibria under the set of parameters

given by Table 5.

7.2 Simulations with Destruction and Harvest

Next, we consider wrasse, coral and CoTS biomass separately under the effects of harvesting or destruction. In order to be able to study the quantitative effects of harvesting and destruction we select cases where $h = 0.008$ and $d = 0$ or $h = 0$ and $d = 0.008$ for each one. We also consider a case where $h = 0.008$ and $d = 0.008$. Each case is plotted together with the same plot seen in Figure 3(a) in order to compare them directly.

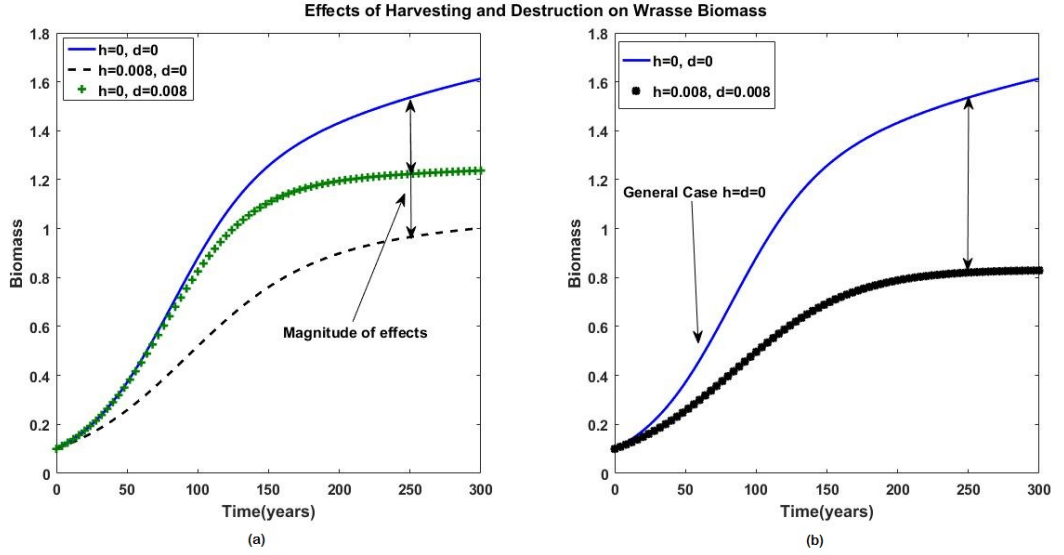


Figure 4: Comparison on harvesting and destruction effects on wrasse biomass.

Figure 4 shows the effects on wrasse biomass caused by only considering harvesting ($h = 0.008$) or destruction ($d = 0.008$). When comparing the destruction and harvesting plots on Figure 4(a), it is apparent that harvest has greater effect on wrasse biomass than destruction. This result stems from the fact that harvest directly removes the biomass of the wrasse from the environment. Nonetheless, the destruction of coral still has a negative effect on the wrasse. Because the wrasse depends on the coral for shelter, destroying the coral indirectly makes survival more difficult for the wrasse. On Figure 4(b), we see the effects of a combination of harvest and destruction have on the wrasse. We note that the wrasse is most negatively affected when there

is a combination of harvest and destruction. Considering that both harvesting and destruction have direct effects on the wrasse, the direct elimination of wrasse biomass and destruction of its home, it would make sense for the combined effects in the plot to the right to do more overall damage

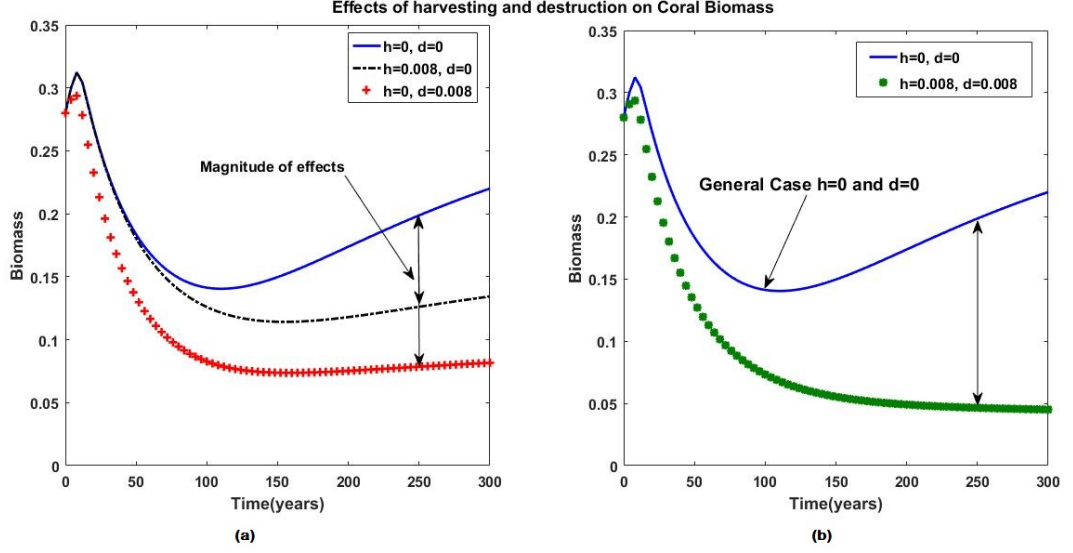


Figure 5: Comparison on harvesting and destruction effects on coral biomass.

Figures 5(a) and 5(b) show us the effects of harvesting and destruction have on the coral biomass. Figure 5(a) gives us two results, one where we only consider harvesting ($h = 0.008$) and another where we only consider destruction ($d = 0.008$). Note that the effects of harvesting appear to be considerably less than the effects of destruction. This result seems intuitive, because destruction implies direct removal of coral biomass, whereas harvesting implies removal of the corallivore predator, the Humphead wrasse, which in turn allows the CoTS to eat coral at an accelerated rate. However, Figure 5(b) shows that the combination of destruction and harvesting effects do not appear to amount for something far more critical than destruction alone, rather it simply accelerates the rate at which the coral stabilizes.

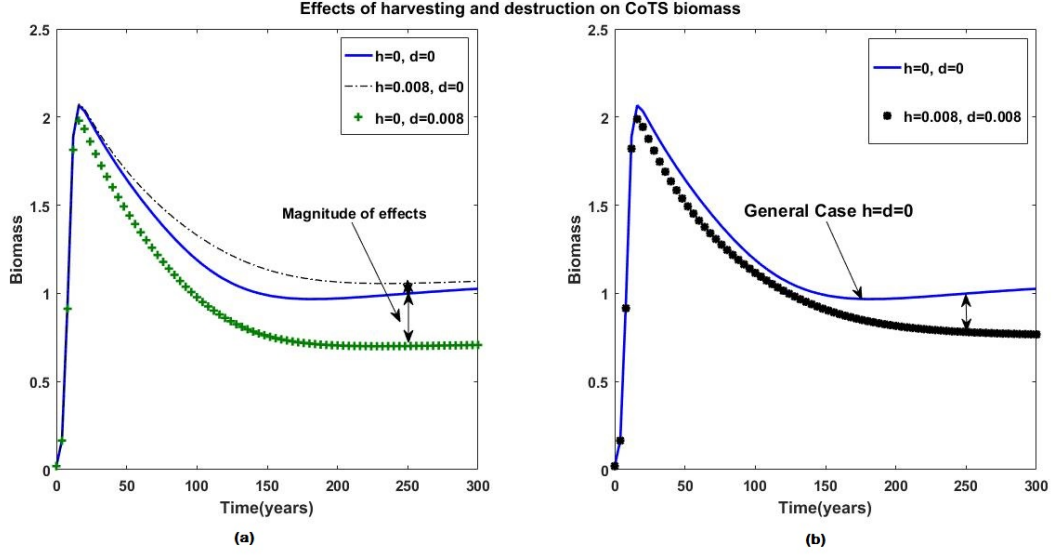


Figure 6: Comparison on harvesting and destruction effects on biomass

Figure 6 shows the effects of harvesting or destruction on the CoTS biomass. Note that, in contrast to Figures 4 and 5, our CoTS biomass actually benefits when only harvesting is considered ($h = 0.008$). This result occurs because of the removal of wrasse biomass. Removing wrasse from the environment removes predators of the CoTS which is what allows their biomass to grow easier. Alternatively, when considering only destruction to coral ($d = 0.008$), the CoTS biomass decreases. Destroying coral eliminates prey of the CoTS that it needs to grow and survive. The elimination of this prey inhibits the growth of the CoTS. On Figure 6(b) we can observe the joint effects of harvesting and destruction. We note that the cumulative effects on CoTS are not as drastic as they were in Figure 4(b) and Figure 5(b) for the wrasse and coral. The CoTS are not affected by the combination of destruction and harvest as the wrasse and coral are, on the contrary, it receives a benefit from it. Figure 6(b) shows that the combined effects actually results in a benefit to CoTS biomass, at least for these particular conditions.

From our various simulations we conclude there are more changes to biomass when considering destruction, rather than harvesting. This is clearly seen in the effects it has on the coral and CoTS biomass. Thus, harvesting affects wrasse the most, since it is a direct intervention. However, for CoTS biomass, although neither harvesting nor destruction affect its biomass directly, it suffers the most from adding destruction effects to the environment.

7.3 Varying destruction and harvesting

In this section, we consider two separate cases for each biomass. One where destruction parameter was set to $d = 0.005$ and plot several simulations where the harvesting parameter was varied between $h = 0$ and $h = 0.03$. In a second case, the harvesting parameter was set to $h = 0.005$ and we also plot several simulations varying the destruction parameter from $d = 0$ and $d = 0.04$. Figure 3 shows a plot of wrasse, coral and CoTS biomasses for each separate case with initial conditions given by $(w(0), c(0), s(0)) = (0.3, 0.5, 0.7)$. In Figure 7, the arrows in the plots specify the direction of flow of parameter values from the $h = [0, 0.04]$. From these plots, we conclude that harvesting practices are more harmful to wrasse and coral but are beneficial to CoTS. The harvesting of the wrasse removes predators of the CoTS and which causes the wrasse's biomass to decline in the environment. The fewer predators there are in the environment, the higher CoTS biomass can achieve which is why they grow to a larger biomass as harvest is increased. On the other hand, the higher the biomass, the more CoTS to predate on the coral which is what makes coral experience a decline in biomass as harvest is increased.

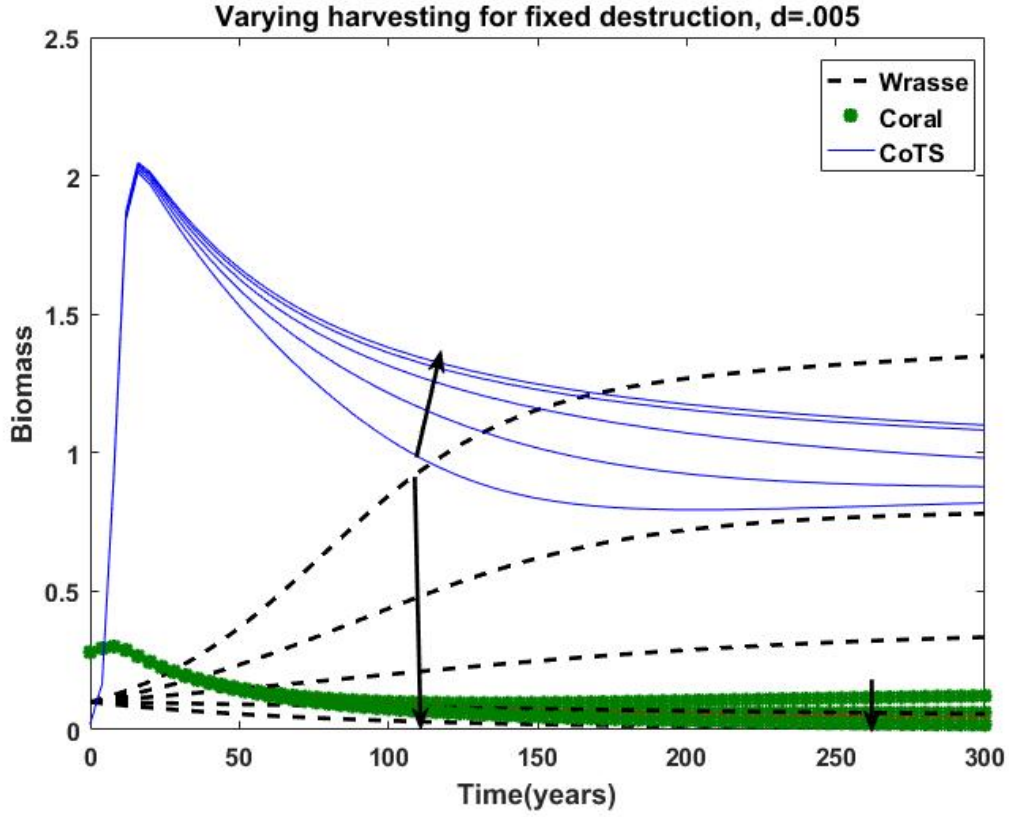


Figure 7: Simulation of wrasse, coral and CoTS for $d = 0.005$ and $h = [0, 0.04]$.

From Figure 7, we can observe the transitional effect of increasing harvesting in a system where there is already a destructive component. Such a system would represent a case where humans develop more efficient, but non-destructive fishing methods. Note that although damage to the coral is minimized as much as possible, there appears to exist a maximal harvesting effort, past which both the coral and wrasse are driven to extinction.

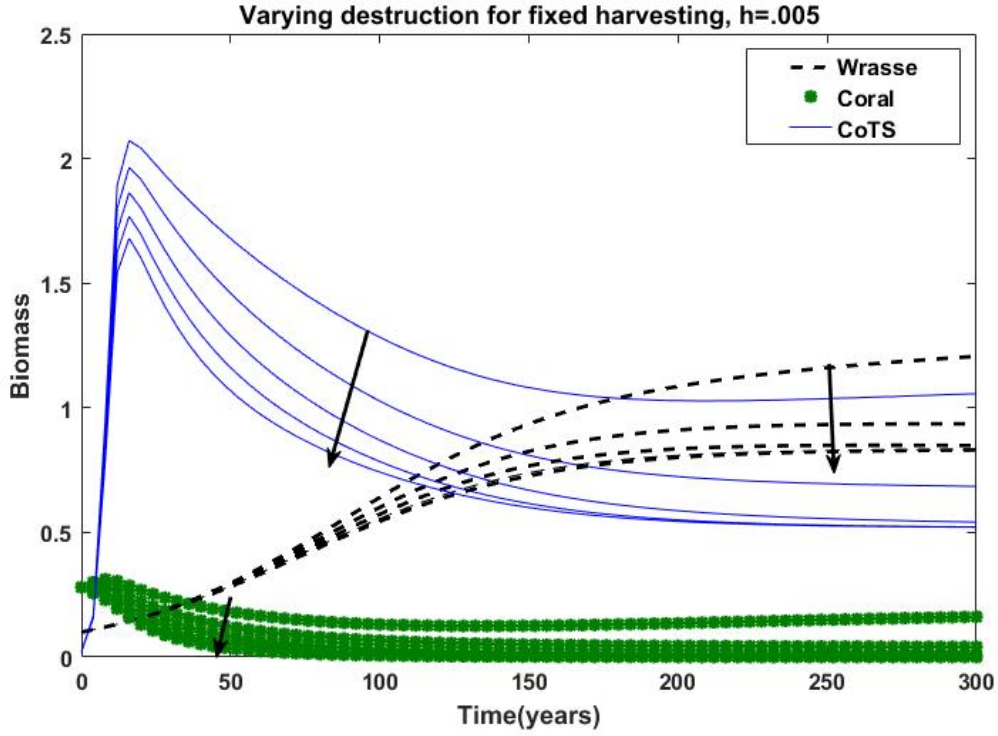


Figure 8: Simulation of wrasse, coral and CoTS for $h = 0.005$ and $d = [0, 0.04]$.

Figure 8 shows the transitional effect of increasing destruction in a system where harvesting is already present. Biologically, this would be a representation of a case where humans made use of more destructive practices, but inefficient fishing techniques that result in a bigger detriment for the environment. In this case case, not only do they fail to harvest wrasse, but utilizing more vicious and destructive methods can cause a chain reaction where the wrasse population decreases, allowing the CoTS to grow and eventually reach a level where it becomes dangerous to the coral and thus, the entire ecosystem.

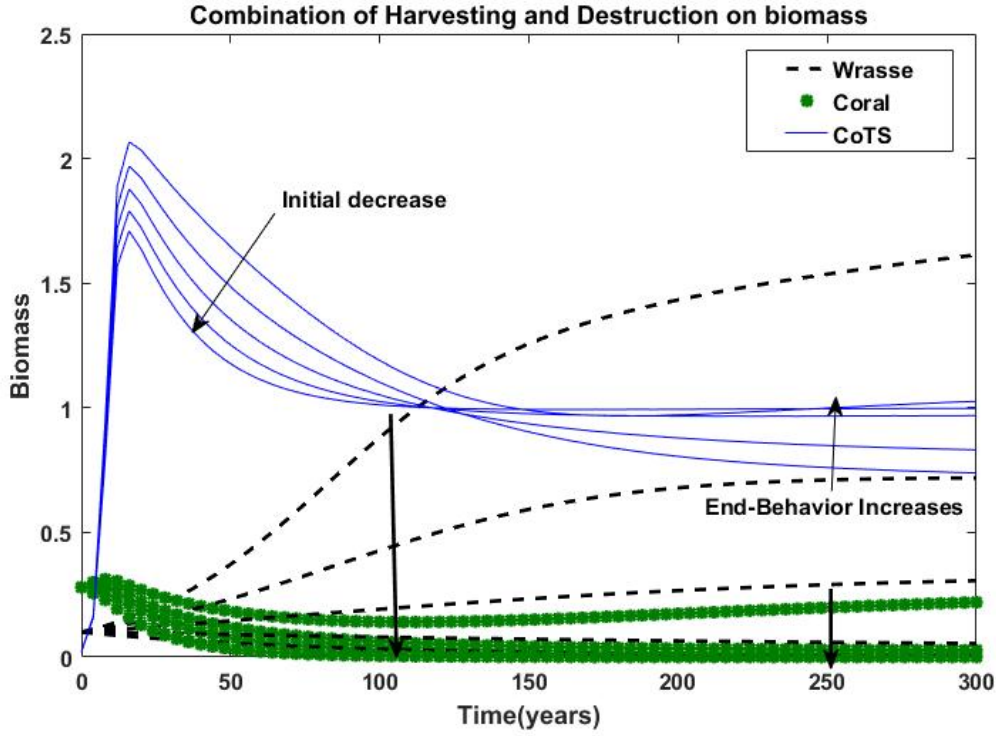


Figure 9: Simulation where harvesting and destruction steadily increase.

Figure 9 plots show similarities with those of Figures 7 and 8, except with a few differences. Note that although coral and wrasse biomass still appear to suffer similarly from incorporating harvesting and destruction, there is a change in behavior for CoTS biomass. From Figure 3(a) and 3(b) we observe that there exists a particular behavior around 100 and 150 years where the CoTS biomass appears to stabilize. Therefore, as harvesting and destruction increases, the initial behavior for CoTS appears to be that of general detriment. However, as time progresses, for higher harvesting and destruction values, an actual benefit to CoTS biomass in the long-run is observed. That is, given that, initially, the wrasse still exists within the environment, which will suppress CoTS biomass progression, but as soon as harvesting increases beyond a certain threshold for the wrasse, it decreases past a point where it cannot suppress CoTS biomass efficiently.

The simulations in this section aid to provide a good intuitive idea as to what to do when it comes to intervening or regulating fishing practices, be it non-destructive or destructive. We conclude that avoiding environmentally harmful fishing methods would prevent further complications. Figure 8 shows that each species is negatively

affected by higher levels of destruction to the coral. Destructive fishing practices inhibit these species from contributing to the coexistence of all of the species residing within the coral reef.

8 Sensitivity Analysis

In this section, we show the sensitivity analysis to determine which parameters have the largest potential effect on the outcome of our model solutions. Determining whether certain parameters have a positive or negative effect on each species in the model will give us insight as to how particular parameters of the model affect each of the species in our study.

Since we are interested in studying how destructive fishing practices affect the ecosystem, we will conduct sensitivity analysis on our destruction and harvest parameters from our non-dimensionalized model (d and h). We will first study the sensitivity of d and h for our coexistence equilibrium in Figure 3, that is under harvesting and destruction practices were used ($d = 0.003$ and $h = 0.008$). The same parameter values listed in Table 5 for all of the following simulations. In order to compare the results found directly, we will conduct the study with $d = h$ with the same initial conditions from Figure 3 ($w(0) = 0.1$, $c(0) = 0.28$ and $s(0) = 0.02$). We expect to find out whether destruction to coral is as sensitive to coral as harvest of wrasse is to the wrasse.

. Since the solution is differentiable with respect to our destruction parameter, d , then in forward sensitivity analysis, we calculate $\partial w / \partial d$ and define the normalized sensitivity index [3]:

$$S_{w_d} = \lim_{\delta d \rightarrow 0} \left(\frac{\delta w}{w} \right) \left(\frac{\delta d}{d} \right)^{-1} = \left(\frac{d}{w} \right) \left(\frac{\partial w}{\partial d} \right).$$

This normalized sensitivity index measures the relative change in the wrasse $\delta w / w$ with a relative small change to the destruction parameter $\delta d / d$.

Sensitivity analysis with respect to d is also performed on coral, c , and CoTS, s . From this process, we obtain three new differential equations that represent changes in population biomass sensitivity index to each respective species over time with respect to d . We then utilize a *MATLAB'S ODE* solver *ode45*, to solve our new three differential equations system simultaneously with the differential equations from our non-dimensionalized system thus our three new differential equations will serve as an adjoint system. We only plot the graphs corresponding to d 's sensitivity indexes and

how it changes over time with respect to each species (wrasse, coral, and CoTS). The way it is interpreted at any time t , is if we were to increase our parameter by 1%, then the effect that each species experiences is given by the product of 1% at time t and the given sensitivity index. We repeat the same process with our harvesting parameter.

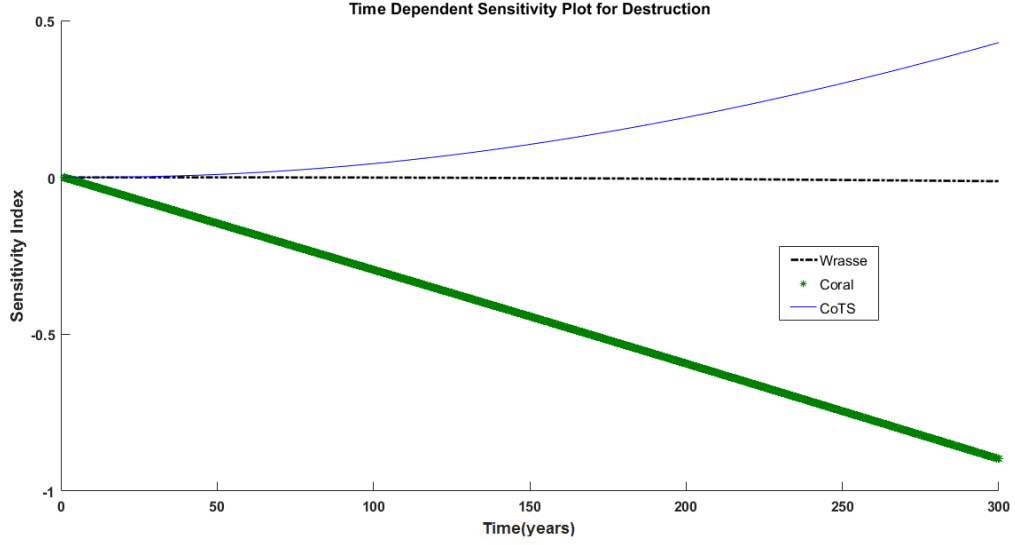


Figure 10: Time dependent sensitivity indexes for destruction where $h = 0.008$, $d = 0.003$ and initial conditions ($w(0) = 0.1$, $c(0) = 0.28$, $s(0) = 0.02$).

Figure 10, provides the corresponding sensitivity indexes of each species to destruction, d , at any given time t . For purposes of accuracy, we selected a time step of 0.001, which plots roughly one data point per hour. A sudden increase in destruction would have very little effect on the wrasse because the wrasse has some ability to survive that is independent of the coral. Coral becomes more sensitive to changes in destruction as the system approaches equilibrium. This event occurs because as the CoTS biomass approaches equilibrium and is kept at a tolerable biomass for the coral by the wrasse, the coral has an easier time tolerating destruction. What is most interesting about this sensitivity analysis is that as the system approaches equilibrium, the CoTS would actually benefit from increased destruction of the coral. This outcome, at first, seems counter-intuitive due to the fact that the coral is the main food supply of the CoTS. However, when considering the fact that coral also increases the carrying capacity of the wrasse, which is a predator of the coral, a very interesting case is discovered. Destruction of the coral would also mean a decrease in additional carrying capacity of the wrasse. So, the fact that the CoTS would benefit from the destruction of the coral means that the loss of predators that comes from the destruction of the coral actually benefits the CoTS more than having more coral in the environment to predate on.

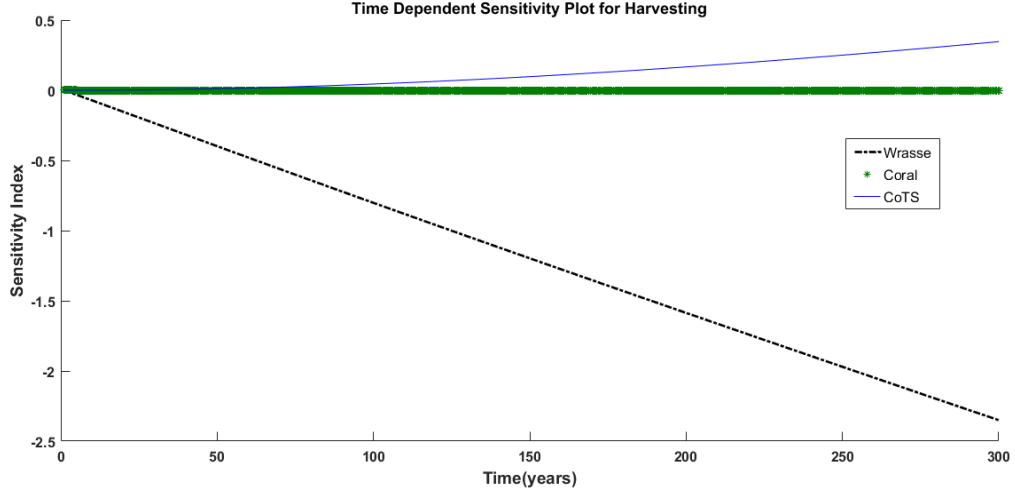


Figure 11: Time dependent sensitivity for harvest, $h = 0.008, d = 0.003$ and Initial Conditions ($w(0) = 0.1, c(0) = 0.28, s(0) = 0.02$).

Figure 11, provides the plots for the changes in sensitivity indexes for each species with respect to harvest, h . These plots provide the changes in biomass for each species for any change in harvest h at any given time t . We observe that it seems as if coral and wrasse have replaced each other. See Figure 10 vs Figure 11.

We then compare the wrasse's sensitivity to harvest to the coral's sensitivity to destruction further under equal rates for harvesting and destruction (Figures 12 and 13). Figure 16 shows that the wrasse is the most sensitive species to changes in rates of harvest. As the system approaches equilibrium, the wrasse approaches an environmental carrying capacity with the level of harvest that has persisted over time. As the wrasse's biomass gets closer to its new environmental carrying capacity that includes harvest, changes in harvest change this carrying capacity. These changes in carrying capacity change the biomass of the wrasse to an extent that is based on how close the biomass of the wrasse was to the previous environmental carrying capacity. Coral is hardly affected directly by changes in harvest because the coral can continue to grow without the wrasse in the environment. The sensitivity index for wrasse is negative because an increase in harvest would remove wrasse biomass at a faster rate. As the system approaches equilibrium, CoTS become more sensitive to changes in harvest. The increase occurs because as each species approaches their environmental carrying capacity that has a certain level of harvest factored in, changes in the level of harvest begin to more directly affect each species biomass. The sensitivity index for CoTS is positive and affects to CoTS because increased harvesting of the wrasse

would eliminate predators of the CoTS and would allow them to grow to a larger biomass.

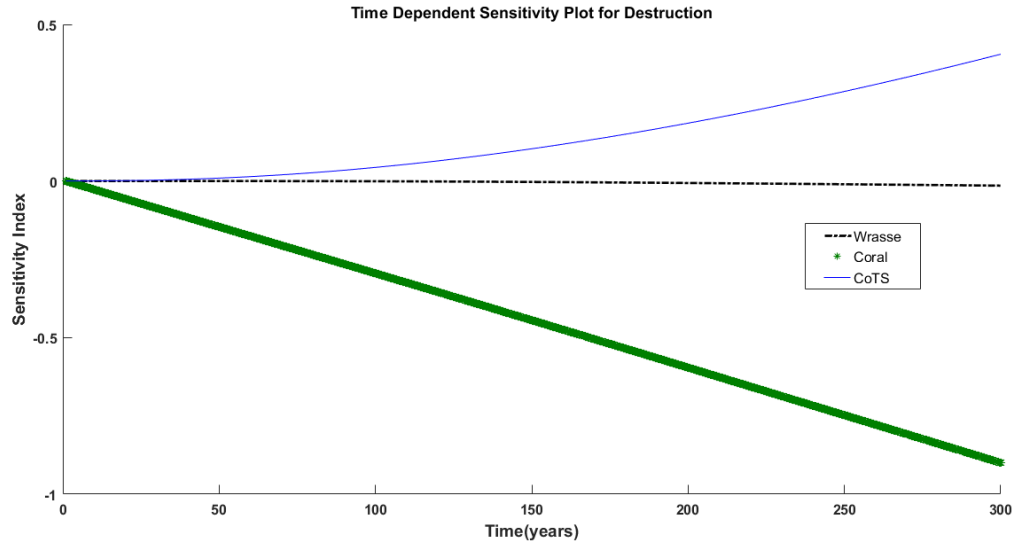


Figure 12: Time dependent sensitivity for destruction, $h = 0.003, d = 0.003$ and initial conditions ($w(0) = 0.1, c(0) = 0.28, s(0) = 0.02$).

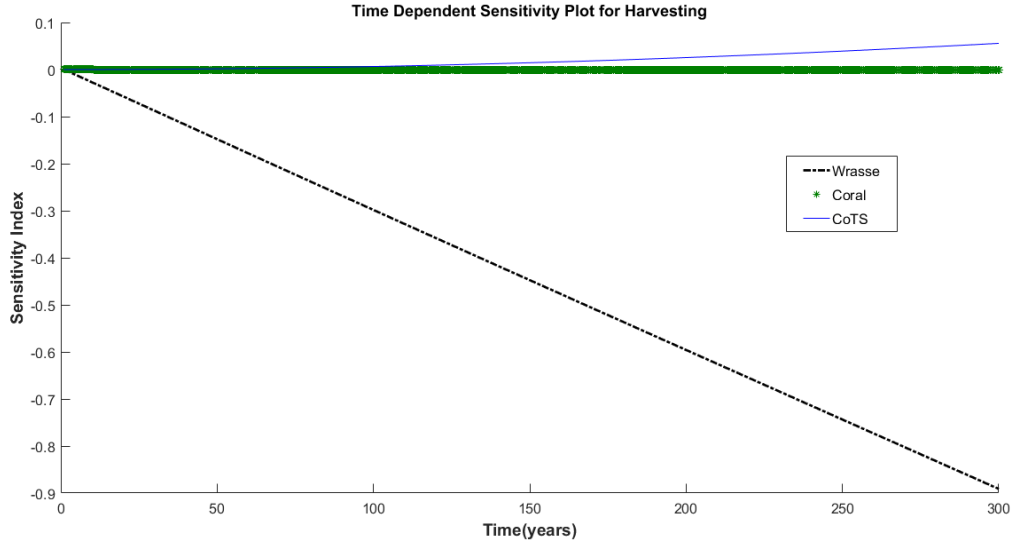


Figure 13: Time dependent sensitivity for harvest, $h = 0.003, d = 0.003$ and initial conditions ($w(0) = 0.1, c(0) = 0.28, s(0) = 0.02$).

We graph the solutions to the equations in the case that $h = d$ so that we may directly compare the sensitivity indexes (Figures 12 and 13). We checked the sensitivity indexes of each species at times 150 and 250 years and recorded the results in Table 6.

Table 6: Sensitivity Indexes for $h = d$ at $t = 150$ and $t = 250$

| Species | Sensitivity | | Values | |
|---------|-------------|-------------|-----------|-------------|
| | 150 yrs | | 250 yrs | |
| | Harvest | Destruction | Harvest | Destruction |
| Wrasse | -0.445 | -0.003 | -0.7422 | -0.0104 |
| Coral | -3.82e-5 | -0.4476 | 0.0001803 | -0.7508 |
| CoTS | 0.01435 | 0.1044 | 0.003905 | 0.2883 |

Considering the fact that we began with the same initial conditions and that harvest and destruction were set to the same value, it makes sense that destruction to coral has about the same magnitude of effect on coral as harvest on wrasse has to wrasse in the ecosystem. We once again note that CoTS benefit from increased

destruction to coral or increased harvest of wrasse for the same reasons written in the explanations of Figures 10 and 11.

From our sensitivity analysis, we observed that CoTS stand to gain from increases in destruction or harvest. However, Table 6 and Figure 10 show that the CoTS would benefit more from an increase in destructive fishing practices because that occurrence would take away from the wrasse's additional carrying capacity more than it would decimate the CoTS main food supply. Sensitivity indexes for wrasse with respect to harvest and coral with respect to destruction suggest that harvest affects wrasse to the same extent that destruction affects coral.

9 Seasonal Harvesting

Fishers in Raja Ampat increase the harvest effort during the northwest monsoon season when the weather is relatively mild, and decrease it during the southeast monsoon season when weather conditions are poorer. In some villages, this seasonality is amplified with the practice of *sasi*, by which restrictions are placed on harvest for a portion of each year to allow fish populations to replenish themselves. Such seasonality is interesting to consider in this model, especially when compared to constant effort harvesting. Therefore, harvest and destruction is modeled through sinusoidal sine function. We then run simulations on *MATLAB*. The proposed seasonality functions for harvesting and destruction functions are given by

$$H(t) = H_1(\sin(2\pi t - 1.5) + H),$$

and

$$D(t) = D_1(\sin(2\pi t - 1.5) + D),$$

where $H_1 = eh$ and $D_1 = ed$ represent the ranges of harvesting and destruction pressure; and H and D represent the portion of total wrasse and coral biomass removed from the system via harvest and destruction in one year. To make results more comparable to those of the constant effort harvesting simulations, these functions are non-dimensionalized by dividing by γ_2 . The functions simplify to

$$h(t) = h_1(\sin(2\pi t - 1.5) + h), \tag{9.1}$$

and

$$d(t) = d_1(\sin(2\pi t - 1.5) + d), \tag{9.2}$$

where $h_1 = eh$ and $d_1 = ed$. The functions give the graphs plotted in Figure 14.

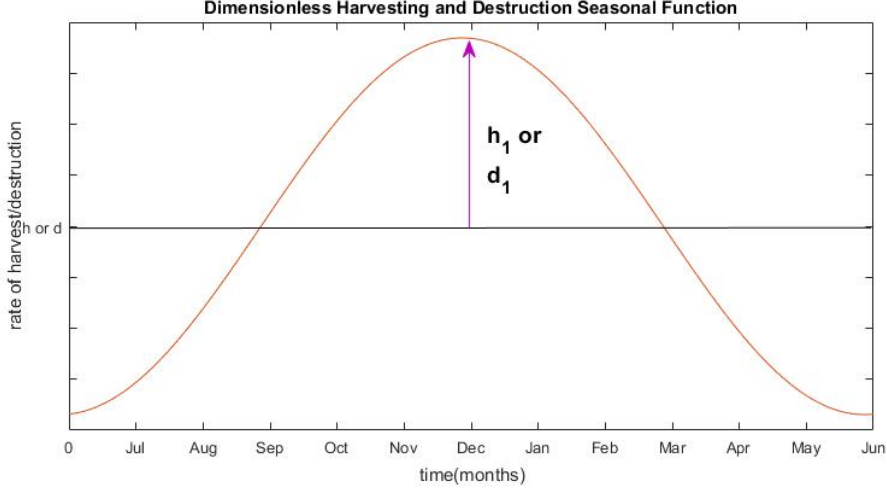


Figure 14: Graph of harvesting/destruction functions

The periods of the functions span a year - starting in July and ending in June. High fishing season, then, is situated in the center of the time interval, in the months October to March. Recall that this corresponds with the mild northwest monsoon season, and also the time during which some villages in Raja Ampat enforce *sasi*.

9.1 Simulations

To compare seasonal harvesting to constant effort harvesting, three simulations will be considered: constant destruction with varying harvest; constant harvest with varying destruction; and constant harvest and destruction. Initial conditions $w(0) = 0.1$, $c(0) = 0.28$ and $s(0) = 0.02$ are used.

Two values for e - in h_1 and d_1 - will be considered. At Boo and Kofiau Islands, researchers observed at most 16 fishing boats and at least 10 fishing boats during the years 2006-2011. Assuming no variation in wrasse catch per boat, we say that there is a 10 : 16 of harvest and destruction during low season versus high season. The harvesting function maximum and minimum values can be written as $h + h_1$ and $h - h_1$. Likewise, destruction function maximum and minimum values can be written as $d + d_1$ and $d - d_1$. Assuming no variation in wrasse catch per boat, we let $\frac{h+h_1}{h-h_1} = \frac{16}{10}$ and $\frac{d+d_1}{d-d_1} = \frac{16}{10}$, giving us $h_1 = \frac{3}{13}h$ and $d_1 = \frac{3}{13}d$, thus, $e = \frac{3}{13}$. This is the first value we consider for e . The second is set as 0.9 for the purpose of exploring how *considerable* difference between high and low seasons affect biomasses. We first consider varying d and h , respectively, when $e = \frac{3}{13}$.

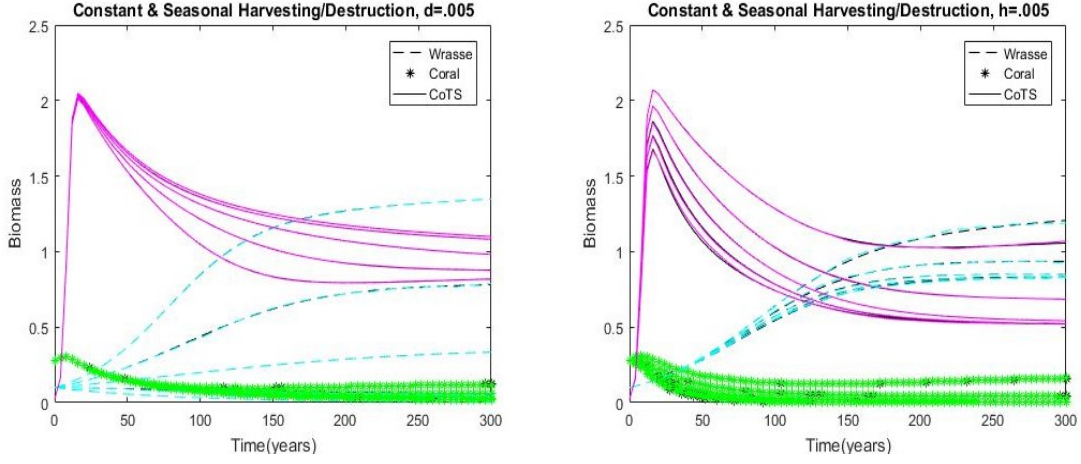


Figure 15: Comparison between varying d and varying h for $e = \frac{3}{13}$. Lines indicated in the legend correspond to constant effort harvesting, while the magenta, green, cyan lines correspond to seasonal harvesting.

We next consider varying d and h , respectively, when $e = 0.9$.

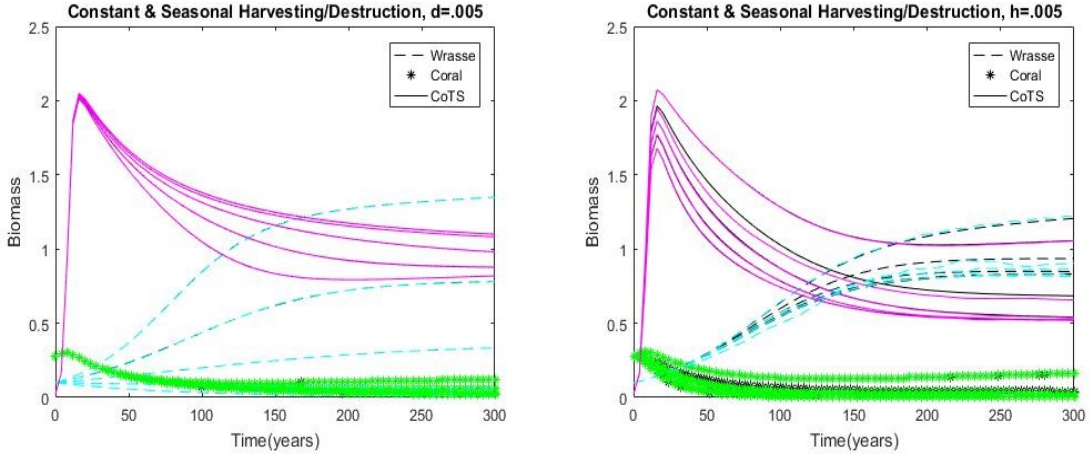


Figure 16: Comparison between varying d and varying h for $e = 0.9$. Lines indicated in the legend correspond to constant effort harvesting, while the magenta, green, cyan lines correspond to seasonal harvesting.

There appears to be little difference in trends for seasonal harvesting versus for constant effort harvesting over time. The largest difference, though slight, is in wrasse

biomass for $e = 0.9$ and varying d .

We next consider the case when $h = d = 0.008$ for both $e = 0.9$ and $e = \frac{3}{13}$.

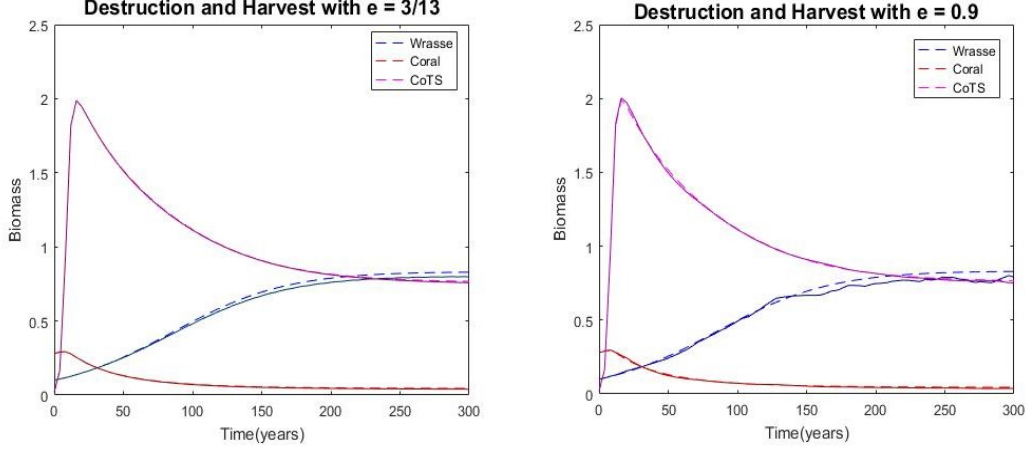


Figure 17: The dashed line denotes constant effort harvesting, while the solid lines result from seasonal harvesting

Wrasse appears to be the most affected by seasonal harvesting and destruction. Seasonality drives wrasse biomass to a lower equilibrium biomass than constant effort harvesting does, and more-so for $e = 0.9$ than for $e = \frac{3}{13}$. When $e = 0.9$, less harvesting and destruction during low season, and more during high season. The decrease in wrasse biomass over time may be due to the low fecundity of the wrasse, given that it is such a long-lived fish. Populations are slow to rebound after any disturbance, and this periodic disturbance at high levels - both from wrasse harvesting and destruction of its habitat - could be damaging to wrasse biomass over time. That said, the difference is quite small, almost to the point of being negligible. More numerical analysis, in addition to mathematical analysis, will have to be done on the seasonal harvesting model in the future for any conclusions to be made regarding it.

10 Discussion

Coral Reefs in the Indonesian Province, Raja Ampat, are experiencing a decline in coral coverage. Lack of predation on Crown-of-Thorns Seastars - due to the overfishing of predators beneficial to the coral reefs such as the Humphead wrasse - and destruction by blast and cyanide fishing have devastated many coral reefs.

Our simulations showed that increases in wrasse fishing lead to increases in CoTS biomass. This increase in CoTS biomass also leads to an increase in coral predation. Therefore, overfishing indirectly leads to a more rapid depletion of the coral by CoTS predation. Our sensitivity analysis also shows that CoTS would benefit greatly from a sudden rise in fishing of the wrasse. This result stems from the wrasse predating on CoTS at a rate that keeps their biomass at a level that is tolerable to the coral.

We also found that destruction of the coral by blast and cyanide fishing has the largest effect on the system as a whole. Our simulations showed that because the coral supports both the CoTS and the wrasse, higher levels of destruction indirectly hurt both the CoTS and the wrasse. However, our sensitivity analysis showed that the CoTS would benefit more from an increase in destruction of the coral over an increase in the harvest of its predator, the wrasse. This event must occur because the destruction of the coral near equilibrium must limit the carrying capacity of the wrasse greatly. As a result, CoTS are enabled to grow to a higher biomass from the decrease in predation, despite having less prey in the environment.

While overfishing and destructive fishing practices do considerable damage to the system, our study shows that blast and cyanide fishing are factors that need to be controlled. These practices, if left unchecked, can damage the coral reef beyond its ability to recover. Also, a sudden rise in the use of these methods are factors that contribute to coral being depleted by CoTS predation.

In conclusion, because destructive fishing practices are more harmful to the system, measures should be taken to limit these practices as much as possible. Implementing more efficient methods of enforcing the law against illegal, unreported, and unregulated (IUU) fishing practices would benefit the reef greatly. Limiting destruction would allow these fishermen to continue in their profession while also keeping from disturbing the natural balance of the system considerably.

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