BIOEE 3620: Term Paper

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1 Introduction

Coral reefs are among the most biodiverse and productive ecosystems on the planet, providing essential ecological services such as coastal protection, habitat for marine species, and resources for human livelihoods. Despite their importance, coral reefs are increasingly vulnerable to a range of stressors including climate change, pollution, overfishing, and extreme weather events. These stressors can disrupt the delicate balance of coral reef ecosystems, leading to significant declines in coral cover and biodiversity. To effectively conserve and manage coral reefs, it is crucial to understand the mechanisms that drive their stability and resilience. One critical area of research in this context is the study of feedback mechanisms and their role in maintaining or disrupting the equilibrium of coral reef ecosystems.

Feedback loops are fundamental to the dynamics of coral reef ecosystems. Positive feedback loops occur when changes in one component of the ecosystem amplify further changes in the same direction, potentially leading to runaway effects and abrupt transitions between different states. In contrast, negative feedback loops act to stabilize the system by counteracting changes and promoting equilibrium. These feedbacks arise from complex interactions among species, abiotic factors, and human activities. In ecosystems characterized by alternate stable states, positive feedbacks are particularly important as they can drive sudden shifts from one stable state to another in response to gradual changes in external drivers.

The focal paper, *Multiple feedbacks and the prevalence of alternate stable states on coral reefs* (Van de Leemput et al., 2016), addresses the issue of alternate stable states in coral reefs. The authors developed a deterministic model to explore how multiple weak positive feedbacks can collectively cause coral reefs to exhibit hysteresis and abrupt transitions between coral-dominated and macroalgae-dominated states. Their findings underscore the significance of recognizing and managing feedback mechanisms to prevent undesirable shifts in ecosystem states.

One of the most well-documented positive feedback loops in coral reefs involves the interaction between corals and herbivores. Corals provide habitat and shelter for herbivorous species such as fish and sea urchins, which, in turn, help control algal growth through grazing. However, when coral cover declines, the populations of these herbivores also decrease due to loss of habitat. This reduction in herbivore populations leads to less grazing on algae, allowing algal populations to grow unchecked McClanahan et al., 2003. The increase in algal cover further inhibits coral growth and recruitment, creating a self-reinforcing cycle that can push the ecosystem towards a stable state dominated by algae.

Another critical feedback loop involves interactions between herbivores and algae. Overfishing of herbivorous species reduces grazing pressure on algae, leading to algal dominated stable states. This increase in algal cover competes with corals for space and resources, exacerbating the decline in coral cover (Hoey and Bellwood, 2011). This feedback loop can be intensified by changes in the palatability of algae and nutrient availability. For example, some species of algae become less palatable to herbivores as they mature, reducing the effectiveness of grazing and allowing algal populations to expand further. Nutrient runoff from agricultural activities can also enhance algal growth, making it even more challenging for corals to compete. Human activities contribute to these positive feedback loops in various ways. For instance, increased fishing pressure in response to declining fish stocks can further deplete herbivore populations, worsening the effects of overfishing on coral reefs.

Building on the work of van de Leemput et al., this study aims to extend their deterministic model of multiple interacting feedbacks by incorporating stochastic events, such as extreme weather, which are becoming more frequent and intense due to climate change. Extreme weather events, including cyclones and marine heatwaves, can cause sudden and severe disruptions to coral reefs (Puotinen, 2007). By integrating stochastic disturbances into the feedback model, we can begin understanding how stochastic events interact with these feedback mechanisms and predict the conditions under which coral reefs might shift from a coral-dominated state to an alternate state, such as macroalgae dominance.

Understanding the broader impact of variability and unpredictability helps in developing robust conservation strategies that can withstand a range of possible future scenarios, enhancing the long-term sustainability of coral reefs. Insights into these interactions can help predict potential thresholds. Policymakers can use these findings to develop regulations and policies that reduce stressors on coral reefs, such as limiting overfishing (Blackwood et al., 2012). In summary, incorporating stochastic events can help in bridging the gap between theoretical models and practical conservation efforts and work towards broader goal of ensuring the resilience and sustainability of coral reefs.

2 Methods

2.1 Focal Paper Model

The authors of the focal paper (Van de Leemput et al., 2016) first describe a simple model without any positive feedbacks to describe shifts in dominance of corals and macroalgae. The original model describes the dynamics of coral cover (C), macroalgae cover (M), and herbivore abundance (H) through a set of differential equations. Corals and macroalgae are assumed to compete for empty space (S), with cover by corals, macroalgae and empty space summing to 1. The growth of corals and macroalgae was influenced by both external import of constitutents (i_C, i_m) and local expansion rates (b_C, b_m). Mortality of corals is represented by a constant decay rate (d_c) and g mortality of macroalgae by a constant grazing rate per herbivor (g). Herbivores grow logistically with a relative growth rate of herbivores (r) that is independent of local macroalgal cover and their mortality is represented by a constant fishing pressure (f). The model considered interactions between corals and macroalgae, with competition for unoccupied space driving dynamics. The state variables for the model are as follows:

$$S = 1 - C - M \tag{1}$$

$$\frac{dC}{dt} = (i_C + b_C C) - d_C C \tag{2}$$

$$\frac{dM}{dt} = (i_M + b_M M)\, S - gHM \tag{3}$$

$$\frac{dH}{dt} = rH\,(1 - H) - fH \tag{4}$$

The focal paper modifies the above described system of equations such that it has a few positive feedback mechanisms. The key feedback mechanisms included in the model are:

1. **Herbivory-Escape Feedback:** As macroalgae cover increases, the herbivory rate per unit of algae decreases, representing a scenario where herbivores become less effective at controlling macroalgae
2. **Competition Feedback:** Macroalgae directly inhibit coral recruitment and growth, increasing the competition pressure on corals.
3. **Coral-Herbivore Feedback:** Corals provide habitat and shelter for herbivores, which in turn graze on macroalgae, reducing their competition with corals.

The first positive feedback loop involved the relationship between macroalgal cover and herbivory rate. As macroalgal cover increased, the herbivory rate per unit of algae decreased, reflecting a scenario where herbivore consumption saturates when macroalgae are abundant. This feedback mechanism, termed the "herbivory-escape feedback," was modeled using a Holling type II functional response, with a parameter governing macroalgae handling time by herbivores. The parameter n is representing the macroalgae handling time of herbivores. This gives us the ODE for the state variable M:

$$\frac{dM}{dt} = (i_M + b_M M)\, S - \frac{gHM}{gnM + 1} \tag{5}$$

The second positive feedback loop focused on the direct negative effects of macroalgae on coral recruitment and growth. This "competition feedback" captured the idea that interspecific competition could lead to alternate stable states if it exceeded intraspecific competition. The inhibition of coral recruitment and growth by macroalgae was represented by a parameter, with values between zero and one indicating the proportion of macroalgae involved in direct inhibition of corals. To model the competition feedback, a parameter α is used. This gives us the ODE for the state variable C:

$$\frac{dC}{dt} = (i_C + b_C C)\, S(1 - aM) - d_C C \tag{6}$$

The third positive feedback loop explored the indirect relationship between corals and herbivores. Herbivores graze on macroalgae, thereby reducing their negative impact on corals. This "coral–herbivore feedback" assumed a positive correlation between coral cover and herbivore carrying capacity. The strength of this relationship was controlled by a parameter, with values ranging from zero to one. The parameter σ is used for this and it represents a positive relationship between coral cover and herbivore carrying capacity. This gives us the ODE for the state variable H:

$$\frac{dH}{dt} = rH\left(1 - \frac{H}{(1-\sigma)+\sigma C}\right) - fH \tag{7}$$

2.2 Model Extension

I extended the deterministic model developed by van de Leemput et al. by incorporating stochastic terms to represent extreme weather events. I define two additonal parameters *event_rate* & *event_impact* which represent the rates of extreme events and the impact on the death of the population of these events. These parameters were integrated into functions with a coin toss type event where we sample from a uniform distribution between 0 and 1, and the events happen when the sample value is less than the event rate.

I decided to use Monte Carlo simulations to understand the influence of stochastic events on this model. By running a large number of simulations with varying initial conditions and random perturbations, Monte Carlo simulations provide a robust framework to explore the range of possible outcomes and quantify the uncertainty in model predictions. It also helps me assess the resilience of coral reefs to unpredictable disturbances. The initial conditions used for the simulations were $U \sim \mathcal{U}[0.5, 1]$, $M \sim \mathcal{U}[0, 0.5]$ and $H \sim \mathcal{U}[0, 1]$. The parameters for the model were taken from Van de Leemput et al., 2016 and are described in Table 1.

3 Results

3.1 Replication of Focal Paper

Initially, I decided to replicate the results of the focal paper to validate my model construction and simulations. I replicated the ODE system described in (2), (3) and (4) and produced the plot Figure 1. The plots are an exact replication of the focal paper, and helps me validate my model construction before proceeding with other results.

Once you consider the feedbacks, you can find alternate stable states and a hysteris loop at intermediate values of the fishing pressure as seen in Figure 2. I could not find a way to plot the unstable branch which connects the stable branches and proceeded with plotting just the stable branches. One could also see the various simulation points in the hysteris

Parameter	Default Value	Description
i_c	0.05	Coral recruitment rate
b_c	0.3	Coral growth rate
α	0.5	Competition coefficient
d_c	0.1	Coral mortality rate
i_m	0.05	Macroalgae recruitment rate
b_m	0.8	Macroalgae growth rate
g	1.0	Herbivory rate
n	1.0	Herbivory saturation
r	1.0	Herbivore growth rate
σ	0.6	Coral-herbivore interaction

Table 1: Model parameters with their default values and descriptions.

loop if the system is simulated for smaller timespans. I decided not to plot those, and only plot the final states after 1000 timesteps.

3.2 Monte Carlo Simulations of Stochastic Events

We first conduct simulations for a case with extreme event happening but not having an impact on the system in Julia (Rackauckas and Nie, 2017). From the histogram Figure 3, we can see that this fishing rate $f = 0.3$ is a safe rate i.e. there is just one stable state in the upper branch for this particular value of f for the parameters in Table 1. There is no possibility of the shifting of the system into an alternate stable state with low coral abundance at this value of f.

For the same value of f, we introduce the extreme event in our simulations and observe the creation of alternate stable states at this "safe value" of f in Figure 4

For the same value of event_rate and event_impact, I decided to reduce the fishing pressure f and see how the histogram changes. I observed an revert back to a distribution around one stable state with dominant coral abundance. Figure 4

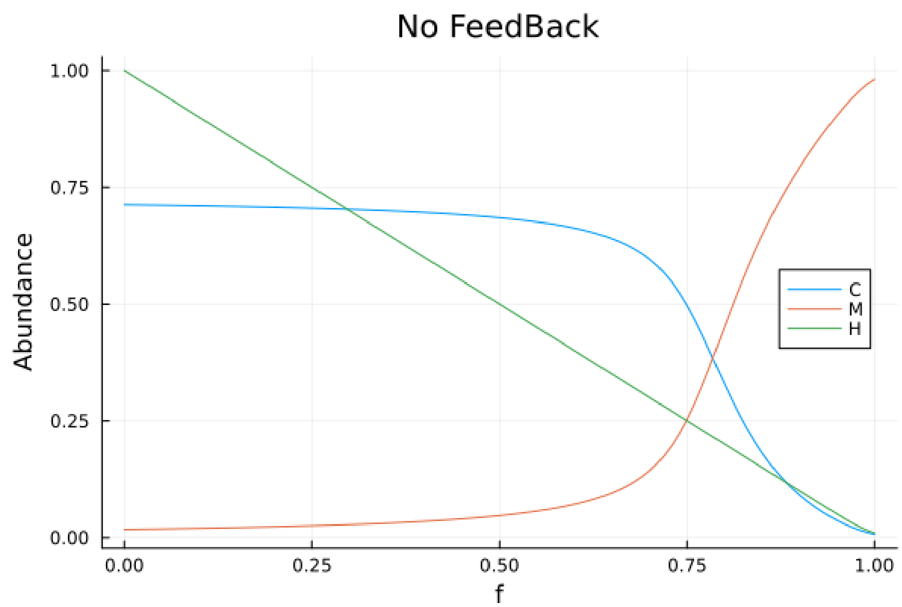

Figure 1: The figure show stable states for the entire system for varying value of fishing pressure in absence of any feedbacks. The y axis is the relative abundance of the state variables.

3.3 Bifurcation Diagrams

The appearance of alternate stable states at a "safe fishing pressure" was investigated using bifurcation plots for system as seen in Figure 6 and Figure 7. We observe a peculiar shifting of the Hysteresis loop to the left in the extreme event case as compared to the case with no extreme event.

The two branches start to overlap at a much lower value of f and increase the chances of a transition from a higher coral abundance to lower coral abundance. It also explains the Figure 5 as shifting the f to 0.1 ensures that the particular value of f has just one stable state.

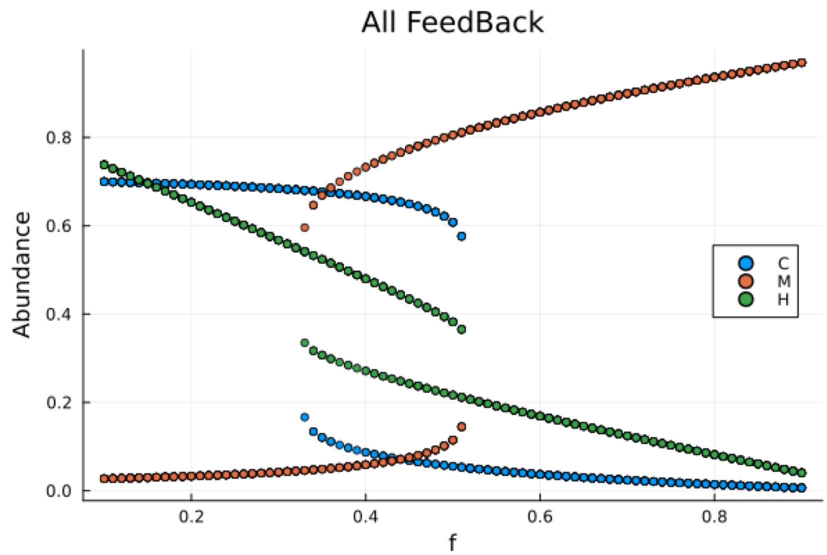

Figure 2: Alternate stable state for the ODE system when feedback mechanism are considered. This figure shows presence of two stable branches for each state variable at intermediate values of fishing pressure f

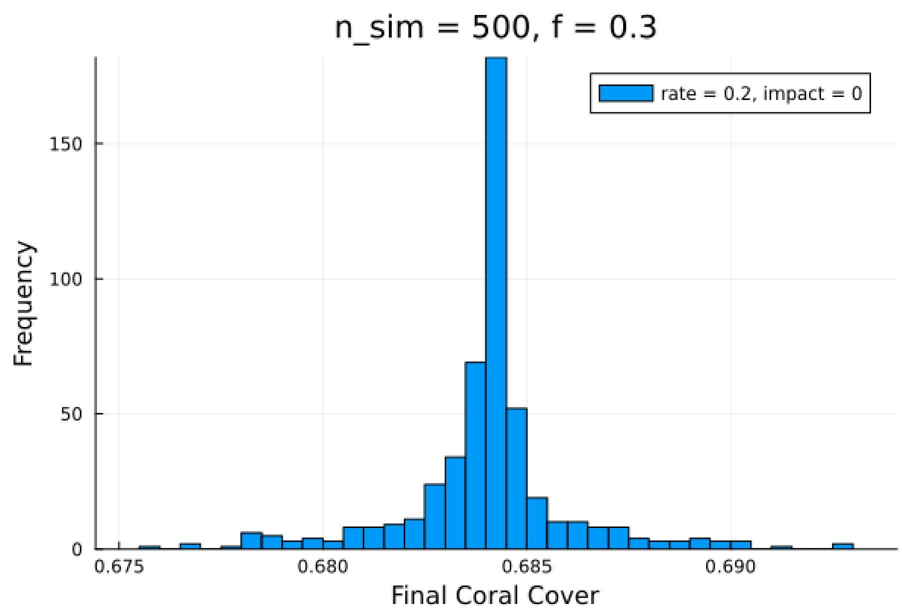

Figure 3: Histogram for final coral abundance with feedback mechanisms for n=500 simulations. This figure shows presence of one stable configuration for a fixed fishing pressure $f = 0.3$. Here event_impact $= 0$ and we observe a gaussian distribution around mean value of 0.684

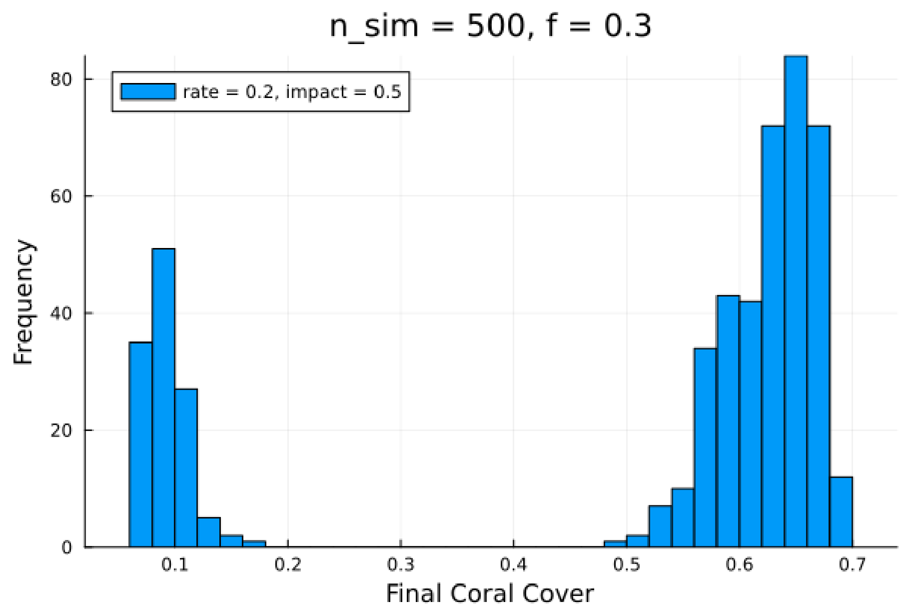

Figure 4: Histogram for final coral abundance with feedback mechanisms for n=500 simulations. This figure shows presence of two stable configuration for a fixed fishing pressure $f = 0.3$. Here event_impact $= 0.5$.

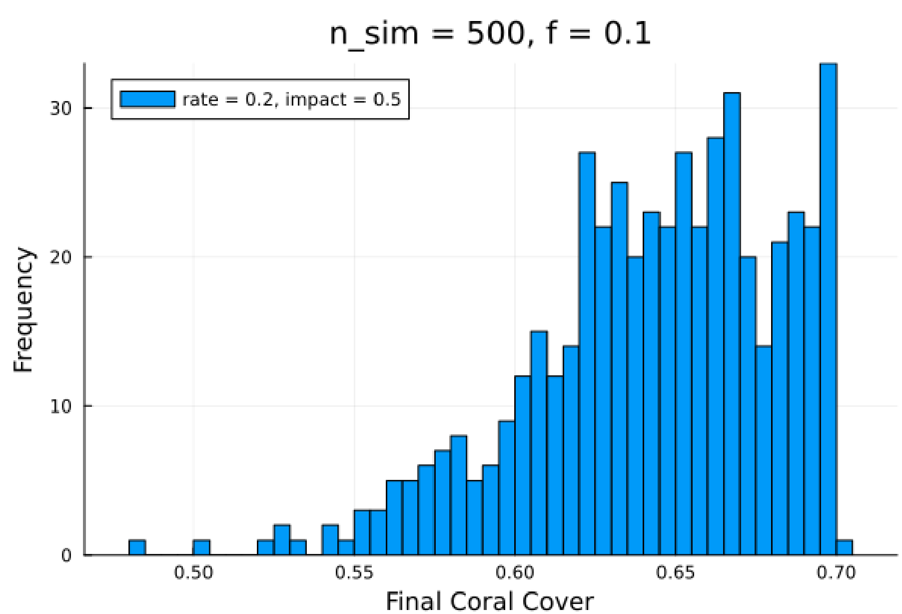

Figure 5: Histogram for final coral abundance with feedback mechanisms for n=500 simulations. This figure shows presence a stable configuration for a reduced fishing pressure $f = 0.1$. Here event_impact $= 0.5$.

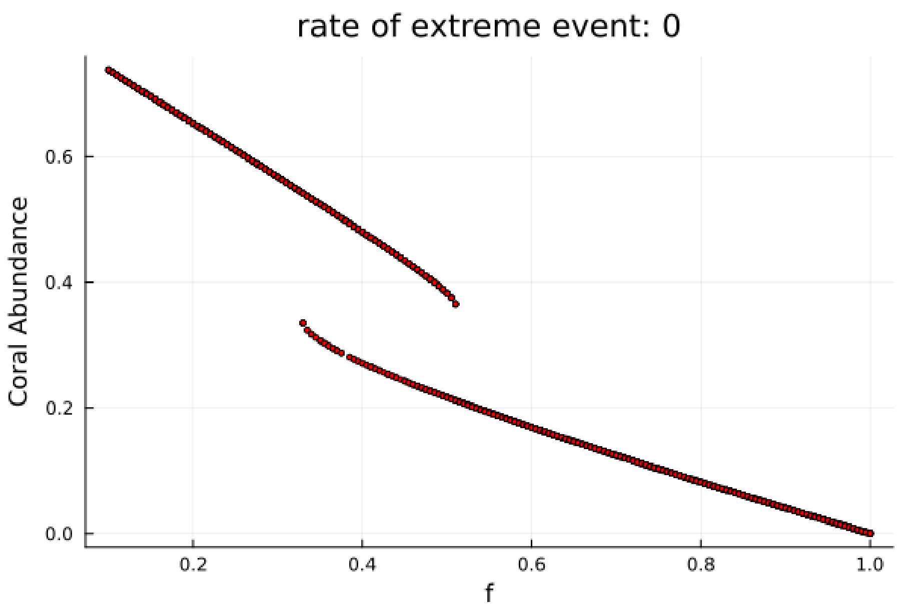

Figure 6: Bifurcation Diagrams for Coral abundance with varying fishing pressure. This diagram has no extreme weather events occuring.

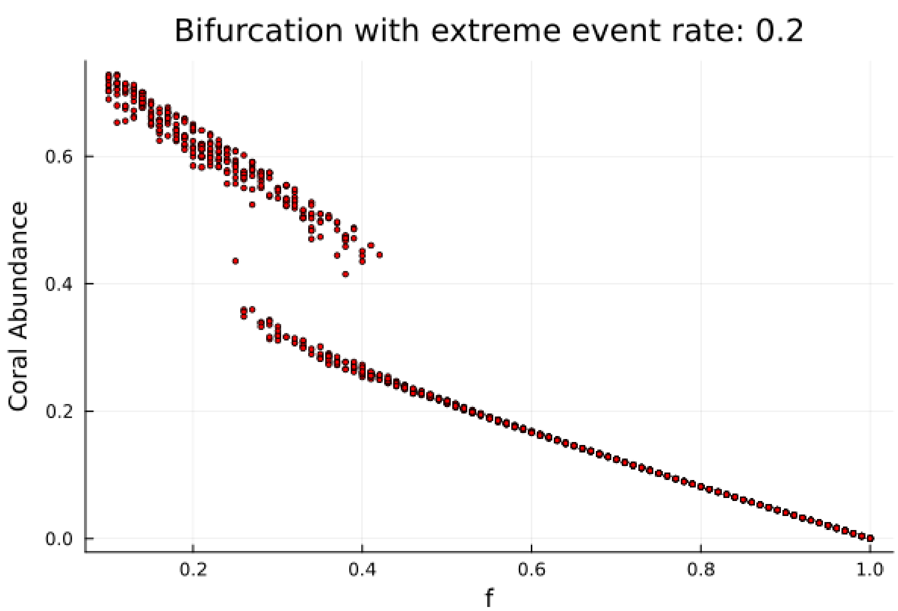

Figure 7: Bifurcation Diagrams for Coral abundance with varying fishing pressure. This diagram has extreme weather events occuring.

4 Discussion

In this study, the main aim was to extend the deterministic model of coral reef dynamics developed by van de Leemput et al. by incorporating stochastic events, such as extreme weather, which are becoming more frequent and intense due to climate change. I utilized Monte Carlo simulations to understand the influence of stochastic events on this model. By running a large number of simulations with varying initial conditions and random perturbations, we explored the range of possible outcomes and quantified the uncertainty in model predictions. This approach was useful to assess the resilience of coral reefs to unpredictable disasters. The findings indicate that stochastic events introduce significant variability in coral cover, reduce the resilience of reefs and increase the likelihood of abrupt shifts to macroalgae-dominated states.

4.1 Main Conclusions

- **Coral Cover Variability:** One of the most significant findings from our simulations is the increased variability in coral cover due to stochastic events at fishing pressures previously thought to be sustainable. The probability distribution of coral cover became bimodal, indicating greater uncertainty and potential for abrupt changes. This increased variability suggests that coral reefs are more vulnerable to fluctuations and less predictable when subjected to stochastic disturbances.
- **Resilience of reefs:** The simulations showed that reefs subjected to frequent and intense stochastic perturbations exhibit lower resilience due to shifting of the hysterisis loop further to the left in Figure 7. It tells us that with increasing rates of extreme weather events with climate changes, we need to revise how we calculated fishing stocks, and how we hand out fishing quotas. The reduced resilience suggests that coral reefs may not recover to their original state as following disturbances, leading to prolonged periods of degraded conditions. Another important consideration is the presence of alternate stable states in isolated reef (lower i_c) makes them extremely susceptible to such abrupt shift for a given fishing pressure. Extra care has to be taken with isolated reefs in the face of climate change, and local fishing pressure has to dynamically adjusted. This has important implications for conservation efforts, as it suggests that measures to enhance resilience, such as protecting herbivores, introducing heat resistant algae (Buerger et al., 2020) and reducing other stressors, are critical for supporting coral reef recovery.
- **Probability of Abrupt Shifts:** The likelihood of abrupt transitions to macroalgae-dominated states increases with the rate of stochastic events. Our simulations revealed that even small perturbations can trigger large shifts in coral cover under certain conditions. This finding highlights the non-linear nature of coral reef dynamics and the presence of tipping points, where small changes can lead to significant and potentially irreversible transitions. This underscores the importance of frequent observation and management of coral reef systems, as it allows for early

intervention to prevent undesirable shifts and maintain ecosystem stability.

4.2 Limitations of the Study

While this study provides insights into the impact of stochastic events on coral reef dynamics, there are several limitations that should be considered:

- The model used in this study is a simplification of the complex interactions that occur in real coral reef ecosystems. For example, it does not account for spatial heterogeneity, species diversity, or other ecological processes that may influence coral reef dynamics.
- The parameters used in the model were based on estimates from the literature, which may not fully capture the variability and uncertainty of real-world conditions. Further analysis is needed to identify the most influential parameters and more empirical data is needed to refine these estimates.
- The stochastic events in our model were represented as random perturbations with fixed probabilities and impacts. In reality, extreme weather events can vary in frequency, intensity, and duration, and their effects may be influenced by other environmental factors.

4.3 Implications

The increased variability and reduced resilience of coral reefs under weather disturbances highlight the urgent need for adaptive management strategies that can respond to changing conditions. Reef management strategies should implement flexible and dynamic approaches that accommodate the uncertainty and unpredictability of extreme weather events. Enhancing the resilience of coral reefs is critical for their long-term sustainability. This can be achieved through measures such as protecting herbivores, reducing overfishing, controlling nutrient runoff, and restoring degraded habitats (of Sciences et al., 2019). Building resilience will help coral reefs recover more quickly and fully from disturbances.

The need for more localised management and monitoring means we need automated systems utilizing artificial intelligence (AI) to play a crucial role in enhancing the resilience of coral reefs (Gonzalez-Rivero et al., 2020). AI-powered sensors and drones can provide real-time data on coral health, water quality, and weather conditions. These automated systems can detect early signs of stress and disturbances, enabling rapid response and targeted interventions. AI algorithms can also analyze vast amounts of data to predict potential tipping points and identify trends, thereby supporting proactive management and timely decision-making.

Local communities are essential partners in the effort to protect coral reefs. Engaging local residents in monitoring and conservation activities enhances the capacity to detect and respond to changes. Community-led monitoring programs can leverage traditional knowledge and local expertise, complemented by AI technologies, to track reef health and report anomalies (Apprill et al., 2023). Training community members in the use of monitoring tools and involving them in data collection and analysis is critical in conservation efforts.

Reducing fishing quotas to protect coral reefs can have significant economic impacts on local communities that rely on fishing for their livelihoods. To address this, it is crucial to implement compensation mechanisms that support these communities. Financial compensation can help mitigate the adverse effects of reduced fishing quotas. Providing training and resources for sustainable aquaculture and eco-tourism can diversify the economic base of these communities and reduce their dependence on fishing. Compensation strategies should be developed in consultation with local stakeholders to ensure they meet their needs.

In conclusion, this study demonstrates the significant impact of stochastic events on coral reef dynamics, highlighting the increased variability, reduced resilience, and higher likelihood of abrupt shifts under extreme weather conditions. These findings underscore the importance of incorporating stochastic disturbances into coral reef models and developing adaptive management strategies to support the resilience and sustainability of these vital ecosystems. Automated monitoring and involving local communities in conservation efforts, coupled with effective compensation for economic impacts, are crucial steps toward achieving these goals.

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