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Modelling the Complex Ecological Dynamics of Kelp Forests

By

JORGE ALBERTO ARROYO ESQUIVEL
DISSERTATION

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DAVIS

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Committee in Charge

2022

To my family, for fostering in me a love to nature and the fellow human.

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Modelling the Complex Ecological Dynamics of Kelp Forests

Abstract

Empirical and theoretical evidence have shown us that ecological systems present a variety of different complex dynamics such as alternative stable states, chaotic dynamics, or long transient dynamics. One of these ecosystems with complex dynamics is the rocky reefs in temperate coastal waters. These rocky reefs exhibit different alternative stable states, of which the kelp forest and urchin barrens are the most studied. Kelp forests generally are highly productive and diverse ecosystems, whereas urchin barrens generally are not. This has made the question of how to manage these ecosystems to preserve current kelp forests an important one. Furthermore, we can use mathematical models to provide important and relevant information for management. In my dissertation, I use mathematical models to explore the complex dynamics that could arise in the kelp forest ecosystem. I focus most of my work on the question of when can kelp spread (i.e. have a positive growth rate at low population densities). I start my dissertation studying how ecosystem engineers' (of which kelp populations are an example) interaction with their environment affect their spread capabilities. Then I explore the possibility of the alternative stable states we observe in rocky reefs are long transients, in which kelp spread would always be feasible in a multi-decadal time scale. Finally, I use a spatially explicit model to explore the question of, when kelp is able to spread in the short time scale, what management strategies can enhance the rate at which it spreads.

Acknowledgments

I want to start my acknowledgements by saying that the notion of me getting a PhD exclusively thanks to my own hard work is misleading and outdated. The truth is this is a journey I have taken together with so many people that thanking all of them for their help would be a Chapter by itself!

Having disclosed my opinion, I want to start by thanking my parents, Jorge Arroyo and Yahaira Esquivel. Not only they invested all their youth on raising me and my sister, but also they are the ones who made it financially possible for me to come to the United States and do my PhD. Even more, all their emotional support while being away from home has been crucial to complete this goal.

I would also like to thank my partner Veronica Suarez. Coming together to do our PhDs, in addition doing so during a global pandemic, has definitely been the biggest challenge of our almost 7 years together. Our time during our PhDs has taught me more of love, patience, and resiliency than I ever planned, and I'm sincerely thankful for that. I hope our life after our PhDs will be much better thanks to all that I've learned by her side.

From the rest of my family, every single person has had a small input on who I am today. However, I would like to give a special acknowledgement to my uncle Oscar Esquivel for boosting my interest in biology and nature. He also gave me his general biology book he used in the 80s to study to become a biologist (solving the mystery of the HIV was the hot topic back in the day!).

I also want to thank my high school teachers Sigifredo Quiros for sharing with me his love for mathematics, and Milenia Arias for sending me into the Biology Olympiads, which ended up being where I learned how much I loved ecology, even though I wasn't that interested in other fields of biology.

I also want to thank my university professors for constantly talking about going to grad school and the importance of getting a postgraduate degree as a mathematician. Especially I would like to thank my undergraduate advisor, Dr Fabio Sanchez, for showing me that working on biology as a mathematician was a real possibility, and helping me do my first research project as a lead author. I am happy to know we are now colleagues and many more joint projects will come in the future.

I am truly grateful of my PhD advisor, Dr Alan Hastings, who believed in me and my potential even before being admitted. Not only that, his help and support over these years has made my PhD experience go the smoothest I could've ever wished for.

The other members of my committee, Drs Marissa Baskett and Fernanda Valdovinos have also treated me as another one of their students, giving me and my projects as much dedication and ambition as they would've to any of their students. Special thanks also to the members over the years of the Baskett and Valdovinos lab for treating me as another lab member as well.

Finally, I want to thank my friends of the Mathematics department that have been there over the years and have supported me as well as them. Most especially, I want to mention Eli Moore, Jason Li, Chenyang Wang, Appilineni Kushal, Dr Samuel Fleischer, Jeonghoon Kim, He Ye, and Shouwei Hui.

Special thanks as well to the staff members of the Mathematics department and the Environmental Science and Policy department through their help on making my life during PhD more organized and cleaner. In particular, I am highly grateful for the help the ESP IT department, who essentially taught me how to use a HPC system and how to solve as an user almost all the issues I may face.

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CHAPTER 1

Introduction

Natural ecosystems are complex dynamical systems. A wide range of complex dynamics have been observed in nature, ranging from predictable oscillations [13] to completely unpredictable chaos [59], including more nuanced dynamics such as alternative stable states and hysteresis (dependence of the system on previous states) [10], and long transients, which resemble attractors for long ecological timescales [57]. In a changing world where ecosystems are being altered by human impacts, understanding what complex dynamics may appear in these ecosystems is crucial to predict the specific impacts of different types of human activities. This includes for example economic activities such as harvesting [122] and ecotourism [17], how ecosystems are impacted by anthropogenic climate change [16], and conservation and restoration [42].

Mathematical models are an useful tool to understand these complex dynamics through dynamical systems theory. Even more, complex dynamics can arise on simple models that can be tractably analyzed through dynamical systems theory. This has been classically exemplified with the logistic map, which phenomenologically models a single population with non-overlapping generations and, with a single equation, can produce chaotic dynamics [94]. More modern models may include more complexity and realism, which may make them not analytically tractable. However, thanks to the modern increased computational power, numerical analysis and statistics allow us to get a better understanding of the complex dynamics arising in these models without the need to analyze them by hand. This has expanded our capabilities of using models to better understand ecological dynamics, and thus make a more robust ecological theory [95].

In this dissertation I focus my work on mathematical models to study the kelp forest ecosystem. Kelp forests are ecosystems created by populations of kelp species and found in many of the rocky reefs of the temperate coastlines of the world [142]. Kelp populations are an example of an ecosystem engineer, which directly modify the availability of resources in the ecosystem by changing the physical properties of some of the biotic and abiotic factors in the system [67]. In the

case of kelp forests, kelp not only provides an energy source for herbivores, it also reduces the light availability of the coastal seabed, which provides shelter to many organisms. This generally fosters highly productive and species-rich communities, which provide direct economical and cultural value to human populations living near the coasts with kelp forests [136], as well as the potential to be a blue carbon sink in some parts of the world to absorb human emissions [75].

Kelp forests have become in recent years an important ecosystem to study for conservation and restoration purposes, as some areas of the world have seen important declines in kelp forest density [76]. Temperate rocky reefs present several population regimes which in practice act as alternative stable states. The most well-researched regimes are the kelp forests and the urchin barrens, which are dominated by populations of urchins overgrazing on available kelp [87]. These regime shifts from kelp forest to urchin barrens are one of the main causes of kelp decline. Even more, this bistability behavior makes management more difficult, as ignoring the complexity of the hysteresis present in the ecosystem may make any management decisions futile [66].

Mathematical models allow us to explore questions such as what determines the hysteresis of the system, or which of a given list of ecological interactions has a bigger impact on determining kelp spread (positive growth rate at low population densities). The answers to these questions can then be useful information to make decisions of restoration management.

In Chapter 2 (published in 2020 in the *Bulletin of Mathematical Biology*) I study more generally the dynamics of ecosystem engineers (of which kelp forests are an example). I use a single-species two-patch model to explore under which conditions an ecosystem engineer is able to spread in a patch if there is an established population in the other patch. Using classical stability theory, I find that for low dispersal rates, alternative stable states arise. In these alternative stable states, the population may or may not spread to the other patch depending on the initial population density in the established population.

In Chapter 3 (published in 2022 in the *Bulletin of Mathematical Biology*) I explore another possible explanation to the alternative stable states point of view of the kelp forest-urchin barren regimes. I use a discrete-time two-species model to study the possibility of these regimes being long transients of multi-decadal oscillations. I identify several long transients present in the model and

use perturbation theory to give analytical approximations of how long some of these long transients are.

In Chapter 4 (currently Under Review in *Ecological Applications*) I provide management-relevant information for kelp forest restoration using a mathematical model. I use a two-species integrodifference equation model to study how fast can kelp forest spread in the short term in a one-dimensional coastline. Using this model I find that kelp spread is not possible for high enough urchin densities. When kelp spread is possible, I also find that focusing management efforts in the shorter-term enhances how fast kelp spreads more than distributing the management efforts over a more prolonged period of time.

Spatial dynamics and spread of ecosystem engineers: Two patch analysis

2.1. Introduction

At a community scale, nontrophic interactions between organisms and their environment are important factors to consider when understanding biodiversity and ecosystem functions present in these environments [49]. However, mathematical models usually focus on biotic interactions, and do not account for the former [58], which are only implicitly considered in the parameters of the model. The concept of ecosystem engineers, introduced by [67], presents certain populations as having nontrophic interactions that significantly modify the ecosystem structure. Thus, when modelling populations of ecosystem engineers, this type of interactions should be addressed.

Previous models have considered this relationship between ecosystem engineers and their environment before [27, 28, 45, 51, 147]. However, the question of what conditions allow for the spread of an ecosystem engineer and what the spatial distribution is on a fine scale have not been thoroughly explored. This is an important question as some of these organisms have invaded exotic ecosystems [69], or play an important role in enhancing biodiversity in their habitat range [22]. [45] looked at a spatial model of ecosystem engineers, but focused on the role that dispersal has on local dynamics. However, this analysis does not consider how other factors play a role in spatial dynamics.

The results from [28] show that, in the case of obligate engineers, their interaction with the environment induces a delayed Allee effect, where small population densities may not be able to modify the environment at a rate enough to sustain its population. In a spatial context, Allee effects can produce a limitation of the range in which the population can be found, an effect known as "pinning" [73]. If the nontrophic interactions are ignored, this pinning effect can be overcome by an increase in population densities [73] or an increase in dispersal rate [65]. For obligate engineers we

have to consider these nontrophic interactions. What effect does the environmental modifications have on the ability of an obligate engineer to spread?

The engineering effects of ecosystem engineers are not always strictly local in space, which makes the effects of nontrophic interactions different from an Allee effect [58]. Species that accrete sediment and raise the "height" of the habitat, such as *Spartina alterniflora* cordgrass would raise the height of the habitat at some distance away from the organism. Flow modifiers in aquatic habitats, such as the zebra mussel *Dreissena polymorpha* would modify flow over some distance. Species that affect the fire regime also would have an effect at some distance away from the engineering organism. How does this nonlocal effect of engineering contribute to spatial dynamics? What are the similarities and differences from a system with a standard Allee effect?

In this paper we explore these questions of interaction between the spatial scale of engineering and organism movement by developing a two-patch spatial model that considers not only the dispersal of the population, but also how the environmental engineering effect spreads. This model is the simplest spatial extension of the nonspatial model that considers both of these spatial phenomena. We then analyze these two spatial factors and the local engineering effect to further understand how these factors play a role in the spread of ecosystem engineers.

This paper is divided as follows. In Section 2 we will present the two-patch spatial model of ecosystem engineers that we use to understand this aforementioned interaction. In Section 3, we analyze this model, trying to reveal what are the minimum conditions that allow the population of ecosystem engineers to spread. This will be done based on the ideas presented in [84]. Finally, in Section 4 we discuss the results and their limitations, and provide future ideas of research.

2.2. Model

The model presented in this article is an extension of the model presented in [28] to two patches connected by dispersal of the organism and spread of the engineering effect. We first describe the original model with a small change in the nondimensionalization, which is more useful for the resulting two patch model. We begin with the dimensional form of the one patch model. Denote the population of the ecosystem engineers as \tilde{N} . The engineering species alters a characteristic

of the environment \tilde{E} , which has a value of 0 in absence of the engineering. The growth of the engineering population and its effect on the environment are described by the equation:

$$(2.1) \quad \begin{aligned} \frac{d\tilde{N}}{d\tilde{t}} &= ((a_0 + a_1\tilde{E}) - (b_0 + b_1\tilde{E})\tilde{N})\tilde{N} \\ \frac{d\tilde{E}}{d\tilde{t}} &= -c\tilde{E} + f\tilde{N} \end{aligned}$$

where a_0, a_1, b_0, b_1, c, f are parameters described in Table 2.1. It is important to mention that the parameter a_0 can be either positive or negative. We will say that the population is an obligate engineer if $a_0 < 0$ and a non-obligate engineer if $a_0 > 0$.

TABLE 2.1. Parameters of equation 2.1.

Parameter	Description
a_0	Environment independent growth rate of population N
a_1	Environment dependent growth rate of population N
b_0	Environment independent death rate of population N
b_1	Environment dependent death rate of population N
c	Environment recovery rate from the engineering effect
f	Environment transformation rate from the engineering effect

In [28], the analysis uses a particular non-dimensionalization. Here we consider a different one. If we let $\tilde{E} = (|a_0|/a_1)E$, $\tilde{N} = (|a_0|c/(a_1f))N$, $\gamma = b_0c/(a_1f)$, $\delta = b_1c|a_0|/(a_1^2f)$, $\varepsilon = c/|a_0|$, $\tilde{t} = t/|a_0|$, we transform the previous equation to:

$$(2.2) \quad \begin{aligned} \frac{dN}{dt} &= (\text{sgn}(a_0) + E - (\gamma + \delta E)N)N \\ \frac{dE}{dt} &= \varepsilon(N - E). \end{aligned}$$

This nondimensionalization has a parameter ε interacting with both N and E , which will let us simplify the analysis of the spatial model. Using this nondimensionalization, we will consider a corresponding two patch model of the system.

Assume that the population is separated into n patches, with varying conditions. Suppose that dispersal between patch i and patch j has a base rate $\mu_{i,j}$. In addition, suppose that the engineering effect of the population in patch j has an indirect effect over the environmental variable in patch i

given by $\eta_{i,j}$. Then, in a similar way to other models such as those presented in [65, 84, 120], the engineering population and its effect on the environment in patch i are described by the equations:

$$(2.3) \quad \begin{aligned} \frac{dN_i}{dt} &= (\text{sgn}(a_{0,i}) + E_i - (\gamma_i + \delta_i E_i)N_i)N_i + \sum_j \mu_{i,j}(N_j - N_i) \\ \frac{dE_i}{dt} &= \varepsilon_i(N_i - E_i) + \sum_j \eta_{i,j}N_j. \end{aligned}$$

In general we will assume that $\text{sgn}(a_{0,i})$ is the same value σ for all i (the population is either obligate engineer or non-obligate engineer in all patches at the same time) and $\eta_{i,j} = \eta_{j,i} > 0$ (the spread of the environmental modification from one patch to another is symmetric and the flow goes from a patch with more environmental modification to another with a smaller environmental modification).

Throughout the rest of this paper we will consider the case with two patches with the same underlying dynamics, in which the dispersal of the population and the spread of the environment modification are not influenced by the environment (i.e $\mu_{i,j} = \mu$ and $\eta_{i,j} = \eta$ for any i, j). Notice that this assumption also considers the patches are identical in size, in addition to its suitability [20]. Based on these assumptions, the model we will analyze is written as follows:

$$(2.4) \quad \begin{aligned} \frac{dN_1}{dt} &= (\sigma + E_1 - (\gamma + \delta E_1)N_1)N_1 + \mu(N_2 - N_1) \\ \frac{dE_1}{dt} &= \varepsilon(N_1 - E_1) + \eta N_2 \\ \frac{dN_2}{dt} &= (\sigma + E_2 - (\gamma + \delta E_2)N_2)N_2 + \mu(N_1 - N_2) \\ \frac{dE_2}{dt} &= \varepsilon(N_2 - E_2) + \eta N_1. \end{aligned}$$

[28] showed that for $\sigma = 1$, the system behaves in a similar manner to the classical logistic growth, and in $\sigma = -1$ the dynamics resemble an Allee effect with delay. In the next section we will focus on the spatial dynamics of the case with $\sigma = -1$, with an emphasis on its issues of spread. In order to do this, we analyze the behavior of the System 2.4 through stability analysis of the equilibria where $N_2 > 0$ if our initial conditions have $N_1 > 0, N_2 = 0$. This analysis will

be done by varying the parameters of interest ε, μ , and η , where the first represents the relation between the local engineering effect of the population and the ability of the environment to recover, and the latter two comprise the organismal dispersal and engineering effect spread. However, any analytical formulation of these equilibria is either intractable or not biologically insightful. To overcome this, we will do the analysis numerically using MATLAB.

2.3. Results

In this section we do an analysis of System 2.4 to further understand the spatial dynamics of obligate engineers. In this case, the nonspatial model implies obligate engineers present delayed Allee effects, depending on their ability to modify their environment at a fast enough rate to make it suitable for survival. We compare and contrast these results with those presented in [65], where the Allee effect is considered without nontrophic interactions. In this case, the ability of a population to spread depends not only on its dispersal rate, but also the strength of the Allee effect the population displays.

2.3.1. Stability analysis. To understand how can a population of ecosystem engineers disperse into an uninhabited patch, we will consider the possible stable equilibria of System 2.4. In equilibrium, we get the following relation between population densities. For $i \neq j$:

$$(2.5) \quad \left(\mu + \frac{\eta}{\varepsilon} N_i^* - \frac{\eta}{\varepsilon} \delta N_i^{*2} \right) N_j^* = (1 + \mu - (1 - \gamma) N_i^* + \delta N_i^{*2}) N_i^*.$$

If we numerically solve this relation by varying the parameters μ and η at the same rate, we get a bifurcation diagram for N_1 depicted in Figure 2.1. Notice that Figure 2.1 is split into two different parts, corresponding to the equilibria near carrying capacity (a) and those near extinction (b). Notice that the top equilibria in Figure 2.1(b) correspond to the Allee threshold identified by [28]. Therefore, we would expect the System to behave as a spatial Allee effect with a delay.

Notice as well that a saddle-node bifurcation occurs at some value μ^c . Although this bifurcation seems to have a codimension bigger than one, as two bifurcations of N_1 occur for the same value of μ , this is in fact a saddle-node bifurcation, as can be seen in Figure 2.2, where the codimension of the stable manifold around the saddle node bifurcation is 1. This saddle node bifurcation and

the symmetric relation of Equation 2.5 gives us a similar result to that of [84]. For small values of the dispersal parameter μ , we get nine different equilibria, as shown in Figure 2.3. As μ increases, the equilibria outside of the line $N_1 = N_2$ collapse into one of the three equilibria inside the line. This implies that for big values of μ , we expect that at equilibrium the only possible scenario is $N_1^* \approx N_2^*$.

Now that we know the asymptotic behavior of System 2.4, how does this bifurcation point μ^c vary as we change the other parameters of interest ε and η ? In Figure 2.4, we freely change ε , and change η as a factor of μ . Notice that as the ratio of η/μ increases, the value of μ^c decreases. This makes sense as the implicit effect of the population at one patch makes the other a more suitable environment, which makes spread easier. With respect to ε , as it increases, the value of μ^c increases as well. Notice that ε increases as the environment recovery rate c increases, or the population becomes less dependent on the engineering effect ($|a_0|$ decreases). As the environment recovery rate c increases, the population will need to disperse faster from a suitable patch in order to provide enough density to make an unmodified patch suitable for living. The fact that as the dependence on the engineering effect decreases, the population needs to disperse faster in order to spread seems a contradictory result. However, notice that as $|a_0|$ decreases, then so do \tilde{N} and \tilde{E} , which implies that the resulting population will also be smaller, and thus less able to engineer a suitable habitat.

2.3.2. Fate of the system in the context of invasive species. Given that for small dispersal rates μ we can find conditions under which spread cannot occur from an established patch, the next question we can consider is under what conditions is the population able to spread? This can be answered from a context of invasive species, more specifically we will consider the ecosystem engineer as a "swamper" invader, introduced in [104]. This type of invader succeeds by having a high initial population density as it enters the novel environment. We can consider this type of invader by increasing the initial condition of N_1 , as we keep the initial conditions of N_2 and E_2 equal to zero (an unmodified, uninhabited patch). For the initial condition of E_1 , we will consider two scenarios: An initial invasion to an unmodified patch ($E_1 = 0$), and an initial invasion to a suitable patch (E_1 at a positive equilibrium, which for the given parameter choices correspond to $E_1 \approx 38.7$).

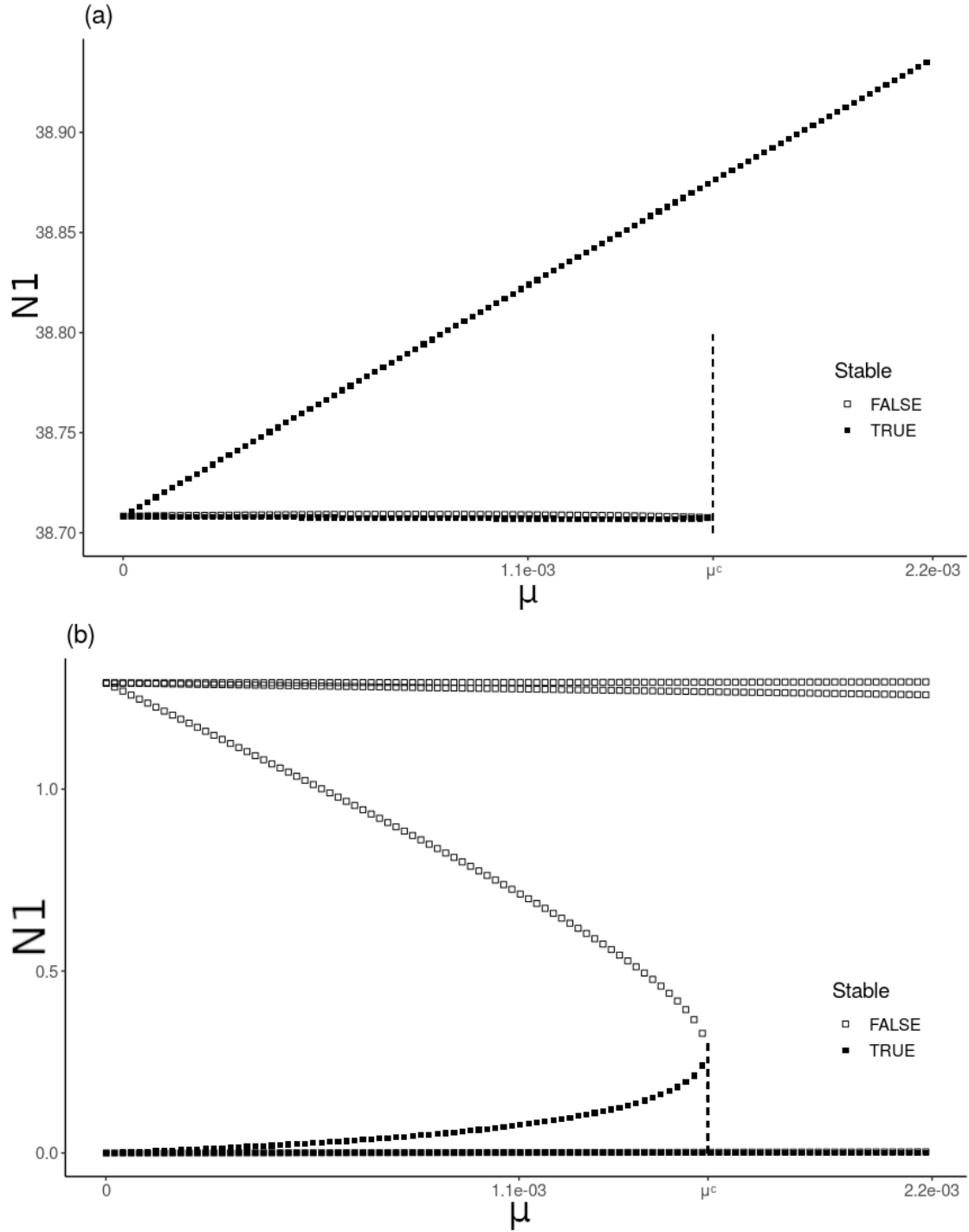


FIGURE 2.1. Projection of the bifurcation diagram of System 2.4 as we vary μ and η over N_1 . The other parameters are $\gamma = 0.2$, $\delta = 0.02$, $\varepsilon = 0.11$, $\eta = \mu$. This bifurcation diagram has two important regions, (a) the values near carrying capacity, and (b) the values near extinction. Notice the saddle node bifurcation at a certain value μ^c .

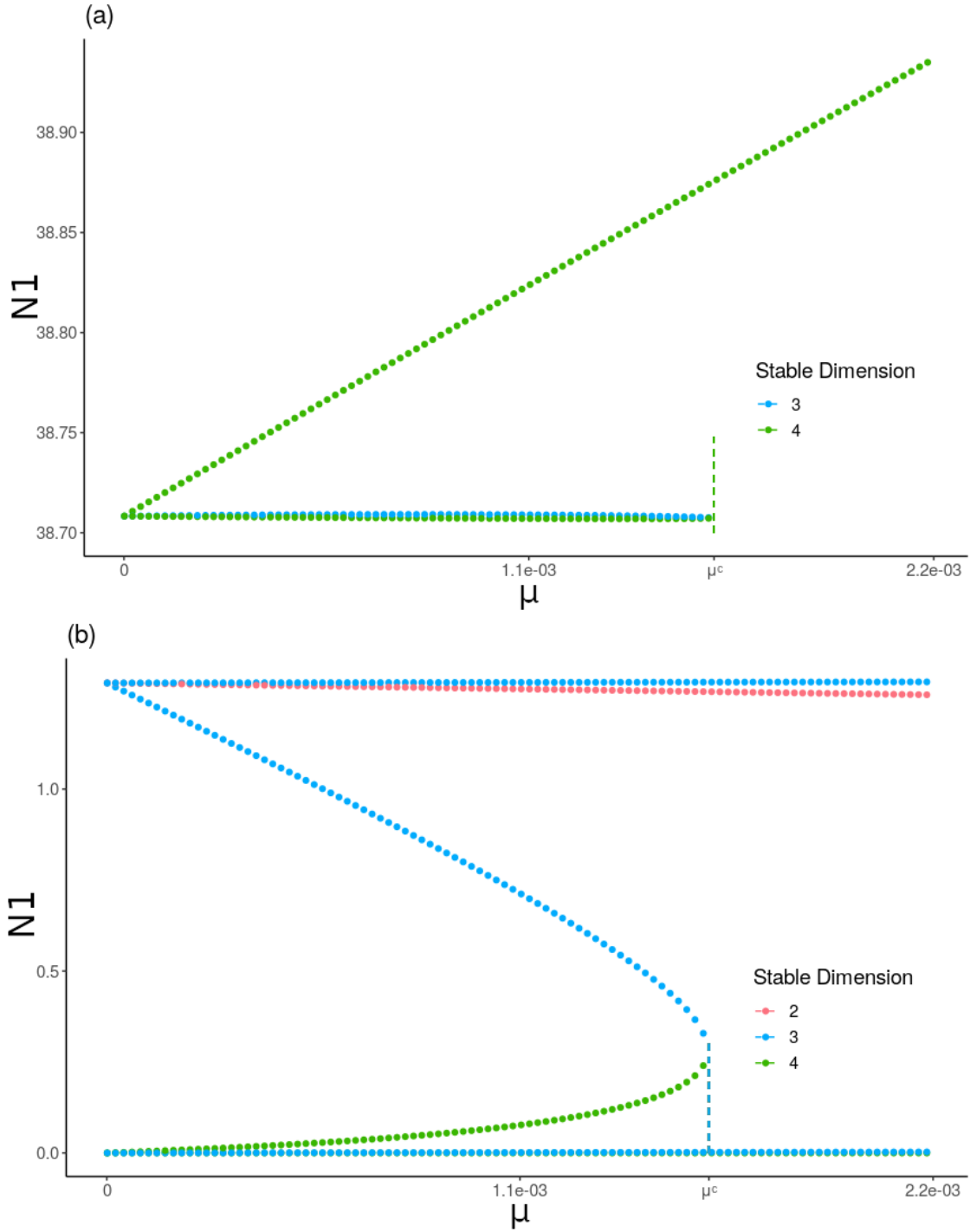


FIGURE 2.2. Dimension of the stable manifold for the equilibria of N_1 in System 2.4 as we vary μ and η . The other parameters are $\gamma = 0.2$, $\delta = 0.02$, $\varepsilon = 0.11$, $\eta = \mu$. This bifurcation diagram has two important regions, (a) the values near carrying capacity, and (b) the values near extinction.

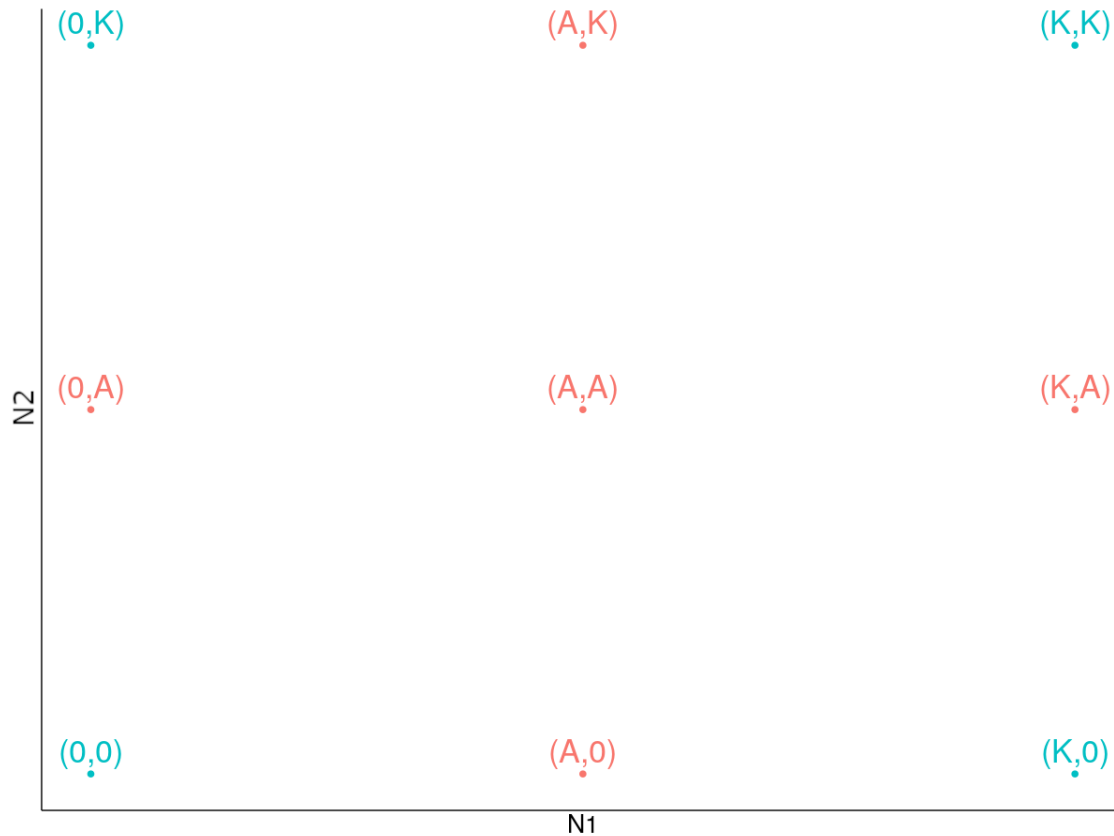


FIGURE 2.3. Possible equilibrium values for small dispersal parameter μ in the N_1 - N_2 axes, where the blue points represent stable equilibria, and the red points represent unstable equilibria. The 0 corresponds to the extinction equilibrium, the K corresponds to carrying capacity equilibrium and the A corresponds to the Allee threshold.

For the scenario of an unmodified patch, Figure 2.5 shows that below the critical parameter μ^c , an increase in initial population density may only lead to a sustained population in a single patch. Notice that after 100 time steps in Figure 2.6, although we are above the bifurcation parameter, it is hard to distinguish the final value of N_2 from that of Figure 2.5. In this case, although the model will eventually spread to the second patch, the system could be passing through a ghost attractor (introduced by [57], where demographic stochasticity could make the spread to the second patch unfeasible).

One way to overcome this could be to increase the initial population density. In Figure 2.7 we explore what is the minimum population required in order to have $N_2(100) > 10$, where 10 is roughly 25% of the carrying capacity value, as we vary freely ε and μ , and vary η as a factor

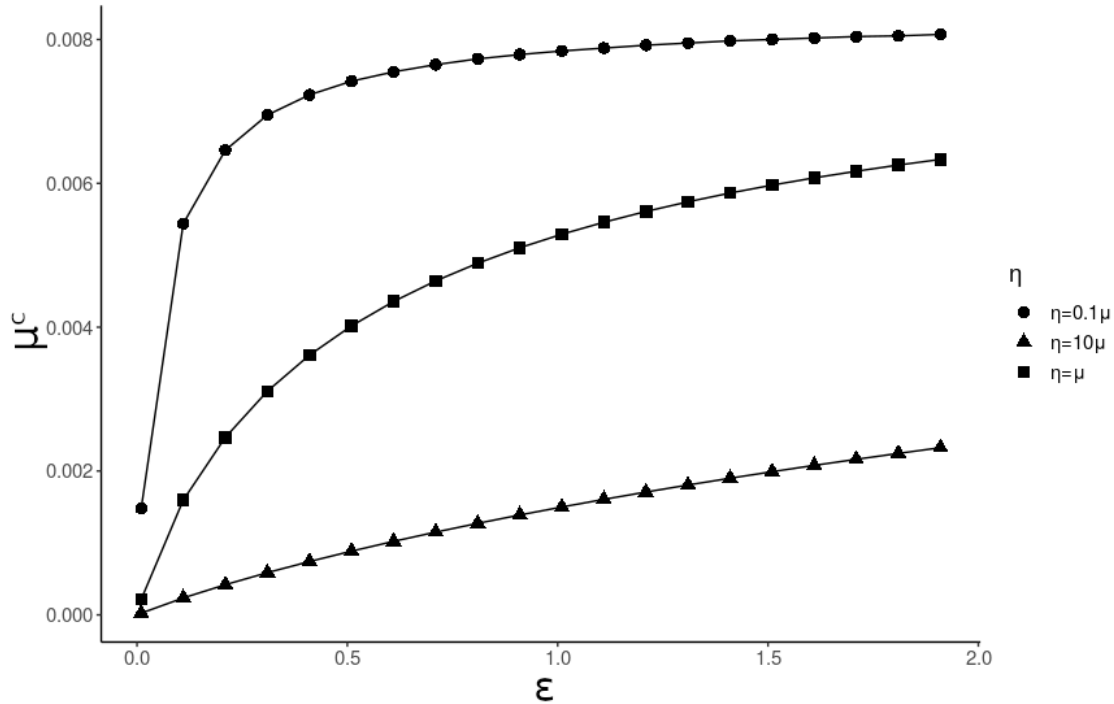


FIGURE 2.4. Values of μ^c for different values of ϵ and η as a factor of μ . In these cases, $\gamma = 0.2$ and $\delta = 0.02$.

of μ . We limit the numerical exploration to $N_1(0) \leq 10^6$, as we consider any population size 4 orders of magnitude higher than carrying capacity would be unfeasible. Figure 2.7 suggests that there is some threshold in ϵ and μ below which the initial population density required to ensure spread becomes orders of magnitude higher than carrying capacity, which suggests spread can be potentially unfeasible.

If we perform the same analysis on an initial invasion to a suitable patch (the case $E_1 \approx E_1^*$), we find that for ϵ, μ above certain threshold values similar to those found in Figure 2.7, spread into the second patch is possible for small values of $N_1(0)$. This suggests that a better environment in the first patch facilitates the population to grow faster, and thus being able to spread with a smaller population density. In addition, this result further reinforces the idea that there exists some threshold of small parameters under which spread is not possible, as spread was not feasible even in a facilitated environment.

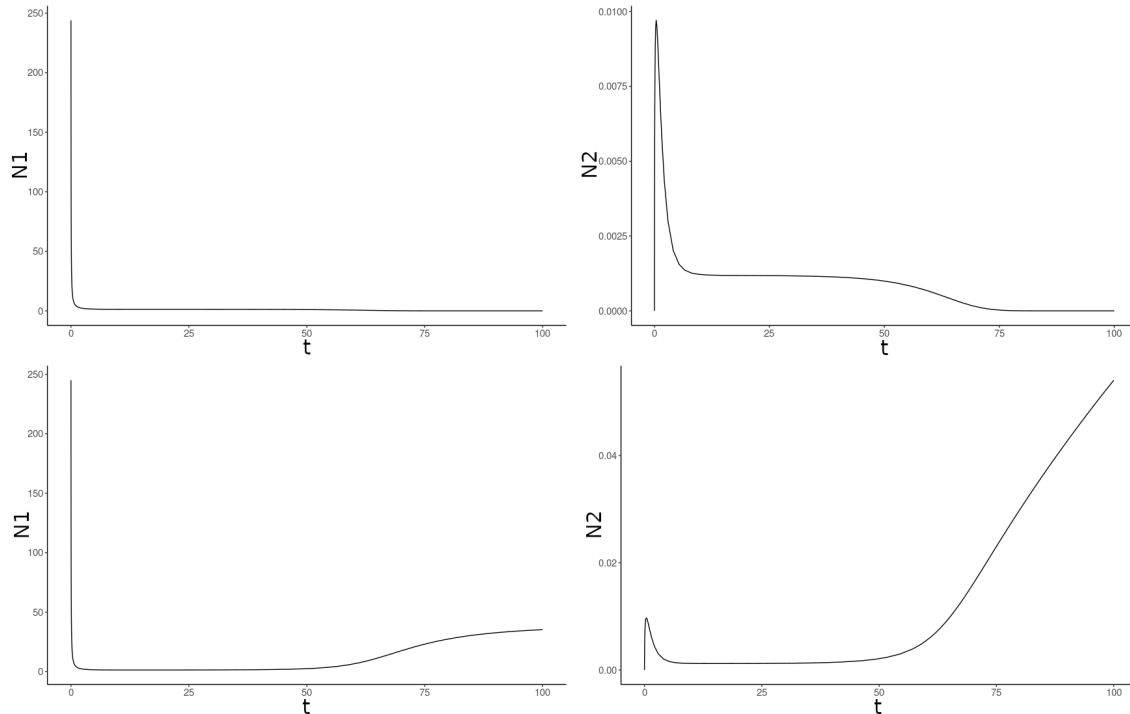


FIGURE 2.5. Solutions for N_1 and N_2 of System 2.4 with parameters $\gamma = 0.2$, $\delta = 0.02$, $\varepsilon = 0.06$, $\mu = 0.0009$, and $\eta = 0.0010$ with initial population $N_1(0) = 244$ (top) and $N_1(0) = 245$ (bottom). In both scenarios we consider $E_1(0) = E_2(0) = 0$. In this case, $\mu^c \approx 0.00091$.

2.4. Discussion

Our analysis of the spatial extension to the model has shown that the key features of the non-spatial model still hold when considering two patches, while also presenting some interesting results by itself. Asymptotically, the system still behaves similar to a system with a delayed Allee effect at the local scale. However, it presents key differences to the spatial extension to the Allee effect model (see [65]). First, there is no clear differentiation between weak, strong, and fatal Allee effects, as the fate of the population depends not only on the initial population density, but also on the suitability of the environment in the invaded patch. This implies that, as we see in Figure 2.7 for a high enough population density it is possible (while potentially unfeasible) to have a rescue effect [3] that allows the spread from one patch to the other. How high enough of a population will depend on how fast is the engineer population able to modify their environment.

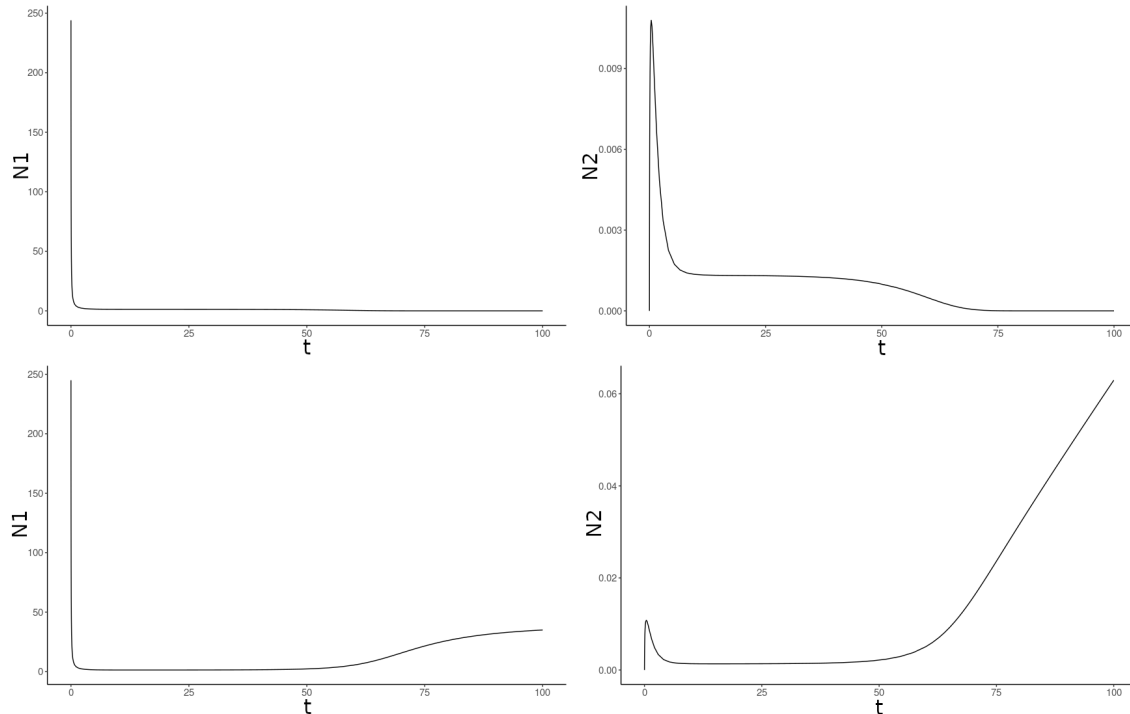


FIGURE 2.6. Solutions for N_1 and N_2 of System 2.4 with parameters $\gamma = 0.2$, $\delta = 0.02$, $\varepsilon = 0.06$, $\mu = 0.0010$, and $\eta = 0.0010$ with initial population $N_1(0) = 244$ (top) and $N_1(0) = 245$ (bottom). In both scenarios we consider $E_1(0) = E_2(0) = 0$. In this case, $\mu^c \approx 0.00091$.

This lack of distinction between the strength of the Allee effect also relates to the other key difference, which is the fact that there is a threshold in the dispersal parameter μ , where over this threshold, the rescue effect will occur as long as the initial patch survives, whereas below it, there may not be a rescue effect at all. Since the Allee effect is delayed, dispersal has to occur fast enough in order for the population to survive before the effect occurs in the population.

These results stand under the assumption that the relative emmigration and immigration rates for the populations are equal on both patches. One way for these rates to differ is that patches have different sizes, which may cause a bigger relative emmigration rate for a smaller patch, or a smaller relative immigration rate for a bigger patch [20]. In this case, a bigger patch would require a bigger immigration rate to persist, as the environment would require a bigger modification in order to be suitable for the population. In contrast, a smaller patch would need a smaller modification rate. This could also be further explored by considering environmental dependences on the dispersal

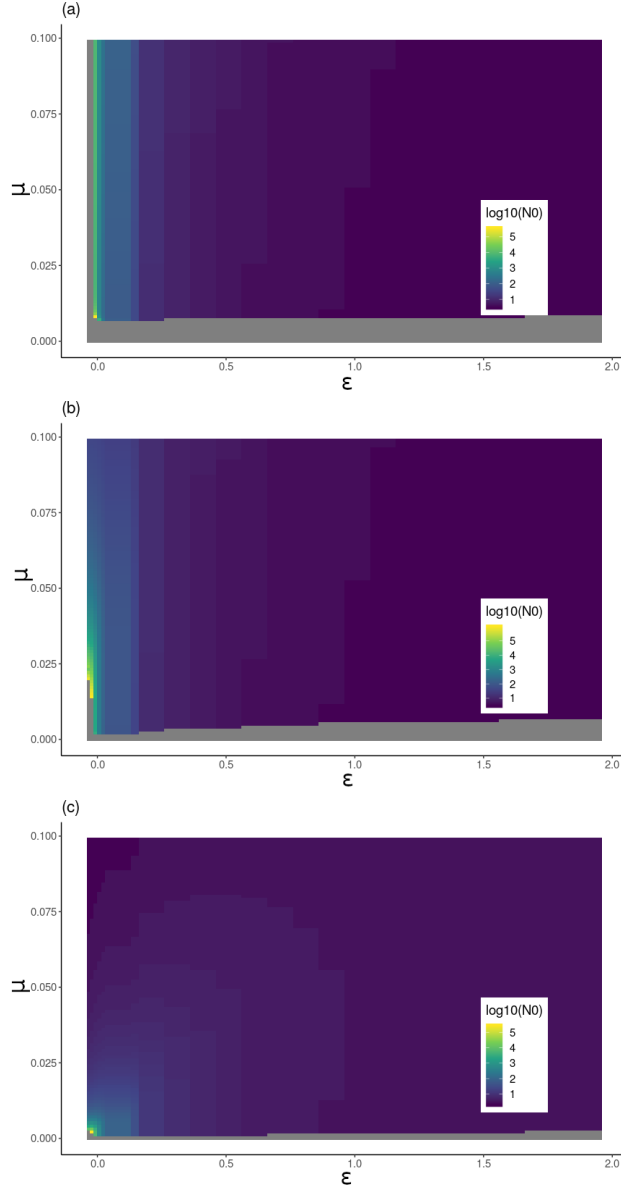


FIGURE 2.7. Minimum initial population density for N_1 (in log scale) required to ensure the population of N_2 is sustainable for high values of μ , where the grey areas represent a value higher than 10^6 (potentially ∞). In this simulation we consider $E_1(0) = E_2(0) = 0$ and take $\gamma = 0.2$, $\delta = 0.02$, and (a) $\eta = 10\mu$, (b) $\eta = \mu$, and (c) $\eta = 0.1\mu$.

rate, where a better environment might make the local populations emigrate less, or a worse environment make them emigrate more.

Another key insight provided in this analysis is the advantage in spreading a population which has a stronger environmental modification at a regional scale. As the order of magnitude of this regional effect increases, the population requirements to spread become less intense. Examples of engineering effects that can be easily spread are modifications in fire regimes [137] or changes in community structure due to water filtration [69]. This study suggests that species performing this type of modification to their environment would be better spreaders in equal conditions to ecosystem engineers doing harder to spread modifications.

Our approach to the analysis has presented several issues. First, a spatial extension with n patches will require $2n$ equations, which as we have seen here, is not analytically tractable for any $n > 1$, which restricts the insights from the analysis to a subset of numerical parameters. Following on that, the other issue this model presents is that the non-dimensionalization used to analyze it does not allow many of the parameters to be easily interpreted or scaled. Here we focus our interpretation on the parameter ε as it represents an useful trade-off between the speed of environmental recovery and the trade-off between dependence on the engineering effect and real population density. However, the numerical scale of these nondimensional parameters in reality is not clear. Our work shows that this scale is important, as the values where the populations may experience a "pinning" effect are only a small portion of our explored parameter space. Understanding the real scale of these parameters would require a further fit to an appropriate dataset.

Some examples of obligate engineers where understanding spatial spread would be of management interest are the mud shrimp [148], the European bee-eater [22], and the *Sphagnum* moss [105]. Increasing the range of these populations can have an important effect in terms of ecosystem function, such as changes in microbial community structure in the seabed, or increased productivity of peatland ecosystems. In the case that the dispersal rate of these populations is low, facilitating their engineering effect by slowing down the recovery of the environment (decreasing ε) would reduce the required dispersal rate to ensure the rescue effects that allow spread. If the dispersal rate is high, spread is significantly simpler, and would be ensured as long as the population is able to persist in the initial patch from which it's spreading.

In terms of species reintroduction, Figure 2.7 shows that this would require an intense population density to be initially introduced in order to ensure spread, in some cases significantly higher than the final carrying capacity of the population. This can be overcome by slowing down the recovery of the environment. This initial population density required might be smaller in the case that the receiving patch is smaller, as the environmental modification would need to be smaller in order to sustain a smaller population in a smaller patch.

Another possible management strategy that would facilitate spread of the population of interest is to artificially engineer the environment before reintroducing the population, which would significantly decrease the initial density required to ensure spread when possible. It is also important to remember that, as presented in Figure 2.6, long transients could arise and have to be accounted for in management decisions. These long transients could be avoided by increasing the initial density introduced. Another possibility to reduce these long transients is by modifying the size of the patch. This could cause an increase between the distance of the relative dispersal rate and the bifurcation value, which would reduce the time of the transient [99]. However, whether it would be required to increase or reduce the patch size to achieve this goal is not clear from this work, and would require further analysis of the system.

Overall, the analysis presented in this manuscript has shown that in the case of obligate engineers, in order to understand the spread dynamics of the population, the spread dynamics of the nontrophic interactions is an important factor to consider and analyze. This idea can be further explored by considering the case in which space is a continuum, which would allow further spatial questions to be understood, such as critical patch size. Other ideas that are not explored in this paper but are important to consider are what are the differences in the dynamics when the population is a nonobligate engineer ($\sigma = 1$ in our model), or if these results hold when considering a discrete time system, where the engineering effect can be spread from one patch to the other. Understanding these ideas would provide a clearer picture of the importance of nontrophic interactions in the spread of natural populations.

Characterizing long transients in consumer-resource systems with group defense and discrete reproductive pulses

3.1. Introduction

One of the goals of mathematical modelling of ecological systems is to understand the fate or long term dynamics of such system. The main method to study such fate has been through the analysis of the attractors in a model [62]. Recent years have seen an increase in the interest of understanding non-attractor dynamics (hereafter transients) of the models, especially those that resemble an attractor for a long period of time (hereafter long transients) [57]. Long transients have gained recognition as a theoretical tool to better describe population dynamics by allowing the study of dynamics that occur in a more biologically relevant timeframe [99]. In addition, an understanding of long transients can inform conservation and natural resource management goals. For example, identifying that a positively-valued long-term behavior observed in nature is actually a long transient and what causes it can guide management to prolong it [44].

Long transients often appear in the presence of a “small” (close to zero) parameter in the model [99]. One of the main challenges of identifying long transients is identifying such a small parameter, which may be a function of the biologically reasonable parameters, and thus may not be easily interpretable. For example, in ghost attractors, this small parameter is the difference between a bifurcation parameter and its bifurcation value [99]. While varying the parameter past such bifurcation leads to the destruction of an attractor, small differences the transient dynamics will resemble the attractor. In crawl-by attractors, the small parameter is determined by the degree to which the trajectory of the system is parallel to the stable manifold of a saddle node equilibrium at a given time [99]. In this case the system will behave similarly to such a stable manifold for a prolonged period of time before the unstable part of the trajectory leads to a change in the system behavior.

One behavior that has been demonstrated to lead to long transients in consumer-resource systems is group defense [135]. Group defense is a behavior where a resource population reduces the risk of individuals being predated by protecting each other. This behavior occurs in diverse animal taxa, which produce early-warning signals to detect predators, as is the case of colonial spiders [132], birds, [117], and mammals [37]. This behavior also occurs in producers such as kelp, where high densities of kelp lead to an increase in predators of kelp grazers, which induces cryptic behavior on such grazers and thus reduces grazing intensity [70].

Group defense transients might also depend on lags in population growth caused by discrete reproductive pulses. In some taxa that exhibit group defense, adult stages of the population may reproduce in discrete, seasonal pulses, such as is the case of kelp [70] or bees [71]. This can provide individuals to a population decades after stressful events which cause population declines, such as competitive exclusion of pioneer species in tropical rain forests [30], or extreme weather events in phytoplankton [41].

In this paper we characterize the long transients in a consumer-resource with both group defense and reproductive pulses. We first construct the model that describes a consumer-resource interaction where the resource exhibits group defense and has discrete reproductive pulses. Then, to illustrate the long transients present in this model, we identify a small parameter that describes each of the transients (crawl-by and ghost attractor), and we use this parameter to calculate the time the system remains in this long transient (hereafter transient time). Finding approximations for these parameters and transient times provides biological insight into how these long transients may arise in natural systems with the modelled dynamics. We conclude this paper with a discussion of these results and their biological implications.

3.2. Model

In this section we construct a consumer-resource model with group defense and discrete reproductive pulses. We previously explored a spatial, non-smooth version of this model to understand spread of kelp being grazed by urchins [7]. We consider the dynamics of adult consumer P and adult resource N densities through time. Adults of population $i = P, N$ experience a natural mortality at a rate d_i . In addition, consider that consumers consume resource following a unimodal

Type IV Holling functional response that represents group defense with a decline in consumption at high resource densities [5]. We let γ_N be the attack rate of the consumer, and the maximum per-capita resource consumption occurs when $N = \frac{1}{\sigma_N}$.

Reproduction and recruitment of juvenile stages occur at discrete points in time. We model this recruitment as a impulsive differential equation. Let $t = m$ be the periods at which the offspring recruit to the population. The number of consumer recruits is proportional to the amount of resource consumed at time $t = m$ with proportionality constant γ_P . Resource produce a per-capita number R of recruits. We assume that $R > 1 - \exp(-d_N)$ in order to have a self-replenishing resource in the absence of consumers. For predation, a fraction of those offspring survive consumption with a probability following an exponential distribution with mean $\frac{1}{\gamma_S}$. Resource offspring also survive intracompetition from adults with carrying capacity proportional to $\frac{1}{\beta}$.

Then, given P_{m+1}^- as the density of consumers before the pulse and P_{m+1}^+ its density after the pulse (with analogous notation for resource, N_{m+1}^- and N_{m+1}^+), the dynamics of the adult consumer and resource populations satisfy the following system of impulsive differential equations:

$$\begin{aligned}
 \frac{dP}{dt} &= -d_P P, \\
 \frac{dN}{dt} &= -\frac{\gamma_N P N}{1 + \sigma_N N^2} - d_N N, \\
 P_{m+1}^+ &= P_{m+1}^- + \gamma_P \frac{P_{m+1}^- N_{m+1}^-}{1 + \sigma_N N_{m+1}^-}, \\
 N_{m+1}^+ &= N_{m+1}^- + R \frac{\exp(-\gamma_S P_{m+1}^-)}{1 + \beta N_{m+1}^-} N_{m+1}^-.
 \end{aligned}
 \tag{3.1}$$

We next transform Model 3.1 into a discrete-time model. We can rewrite the continuous part of the Model 3.1 as

$$\begin{aligned}
 \frac{1}{P} \frac{dP}{dt} &= -d_P, \\
 \frac{1}{N} \frac{dN}{dt} &= -\frac{\gamma_N P}{1 + \sigma_N N^2} - d_N.
 \end{aligned}
 \tag{3.2}$$

Following the derivation of [29], we discretize the System 3.2 as

$$(3.3) \quad \begin{aligned} P_{m+1} &= P_m \exp(-d_P), \\ N_{m+1} &= N_m \exp(-d_N) \exp\left(-\frac{\gamma_N \exp(-d_P) P_m}{1 + \sigma_N N_m^2}\right). \end{aligned}$$

By taking $\delta_P = \exp(-d_P)$, $\delta_N = \exp(-d_N)$ and using $P_{m+1}^- = P_m$ and $N_{m+1}^- = N_m$ as described in System 3.1, we arrive the following discrete-time model:

$$(3.4) \quad \begin{aligned} P_{m+1} &= \delta_P P_m + \gamma_P \frac{P_m N_m}{1 + \sigma_N N_m^2}, \\ N_{m+1} &= \delta_N N_m \exp\left(-\frac{\gamma_N \delta_P P_m}{1 + \sigma_N N_m^2}\right) \\ &\quad + R \frac{\exp(-\gamma_S P_m)}{1 + \beta N_m} N_m. \end{aligned}$$

To simplify our analysis, we will study a nondimensional version of the model. For each m , let $p_m = \gamma_S P_m$, $n_m = \beta N_m$. Then, if $\gamma_p = \gamma_P/\beta$, $\gamma_n = \gamma_N \delta_P/\gamma_S$, $\sigma = \sigma_N/\beta^2$, our nondimensional version of the model is

$$(3.5) \quad \begin{aligned} p_{m+1} &= \delta_p p_m + \gamma_p \frac{p_m n_m}{1 + \sigma n_m^2}, \\ n_{m+1} &= \delta_n n_m \exp\left(-\frac{\gamma_n p_m}{1 + \sigma n_m^2}\right) + R n_m \frac{\exp(-p_m)}{1 + n_m}. \end{aligned}$$

Note that we have also changed the indices of δ_i and k_i in order to preserve clarity.

3.3. Analysis and Results

In this section we characterize the dynamics of Model 3.5 and its potential for long transient dynamics. We identify two different classes of long transients, a crawl-by transient around the extinction of resource and another around the carrying capacity of the resource, and a ghost consumer-resource cycle. To illustrate the transients identified and test the accuracy of our analytical approximations, we also characterize all transients numerically by iterating the logarithm of Model 3.5 in Julia, where the used, fixed parameters and initial conditions are specified as relevant to each analysis below. Based on preliminary numerical simulations in double-precision

floating-point numbers, we find that iterating the logarithm of Model 3.5 instead of the original model prevents numerical instabilities potentially occurring at long-transients near zero by reducing the range of the derivative near zero. The source code for these simulations can be found in <https://github.com/jarroyoe/characterizing-transients>.

We analytically derive approximations for the transient time of the crawl-by transients using perturbation theory, while we numerically analyse the ghost attractor transient time by regressing the transient time using a power law, which we describe further in Section 3.b.

Before we characterize these long transients, we first analyze the equilibria of the model. This model has up to four biologically relevant fixed points: a resource-only carrying capacity equilibrium $(0, n^*)$, an unstable extinction equilibrium $(0, 0)$, and two possible unstable coexistence saddle equilibria (p^\wedge, n^\wedge) . We assume that the carrying capacity of resource is greater than the density at which consumption growth is its highest, i.e. $n^* > 1/\sqrt{\sigma}$, such that group defense is relevant to resource populations below carrying capacity. Under this condition, the equilibria $(0, n^*)$ and (p^\wedge, n^\wedge) go through a transcritical bifurcation at

$$(3.6) \quad \gamma_p^* = (1 - \delta_p) \frac{1 + \sigma n^{*2}}{n^*}.$$

In this case, the equilibria $(0, n^*)$ is stable for $\gamma_p < \gamma_p^*$ and unstable for $\gamma_p > \gamma_p^*$, and the equilibrium (p^\wedge, n^\wedge) is unstable for $\gamma_p < \gamma_p^*$ and is not in the first quadrant (i.e. \mathbb{R}_+^2) for $\gamma_p > \gamma_p^*$. See Appendix A for the expressions of these equilibria and their stability. This analysis allows us to better understand the nature of the transients we have identified.

3.3.1. Crawl-by transients. Although the coextinction equilibrium is a saddle in the n -direction (which implies that n will stay above 0), System 3.5 can resemble a system where the resource is extinct for a long period of time when consumer density is high (Figure 1). This is an example of a long crawl-by transient. We determine how prevalent this behavior is in the following Theorem, proven in Appendix B.

THEOREM 3.3.1. *Let $\varepsilon \ll 1$. If p_0 is of order ε^{-1} and n_0 of order 1, then System 3.5 goes through a crawl-by transient at the extinction of resource $n = 0$. Recovery of resource will begin*

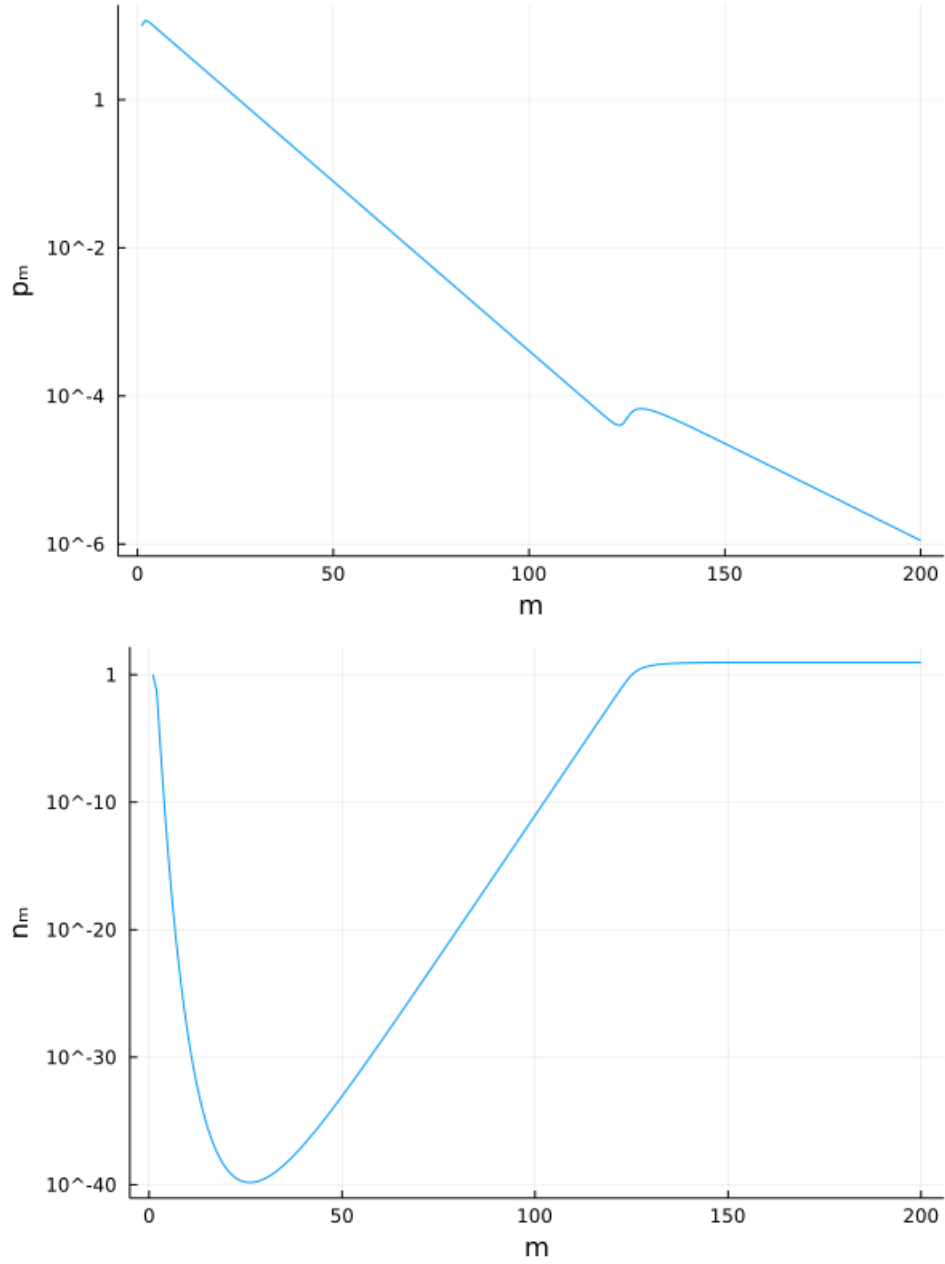


FIGURE 3.1. Time series in logarithmic scale of **a)** consumers p_m and **b)** resource n_m following System 3.5 for 200 time steps (m). In this figure, $p_0 = 10, n_0 = 1, \delta_p = 0.9, \gamma_p = 1, \sigma = 2.67, \delta_n = 0.8, \gamma_n = 1, R = 2$.

after a time of approximately

$$(3.7) \quad M = O\left(\frac{\log(\varepsilon)}{\log(\delta_p)}\right).$$

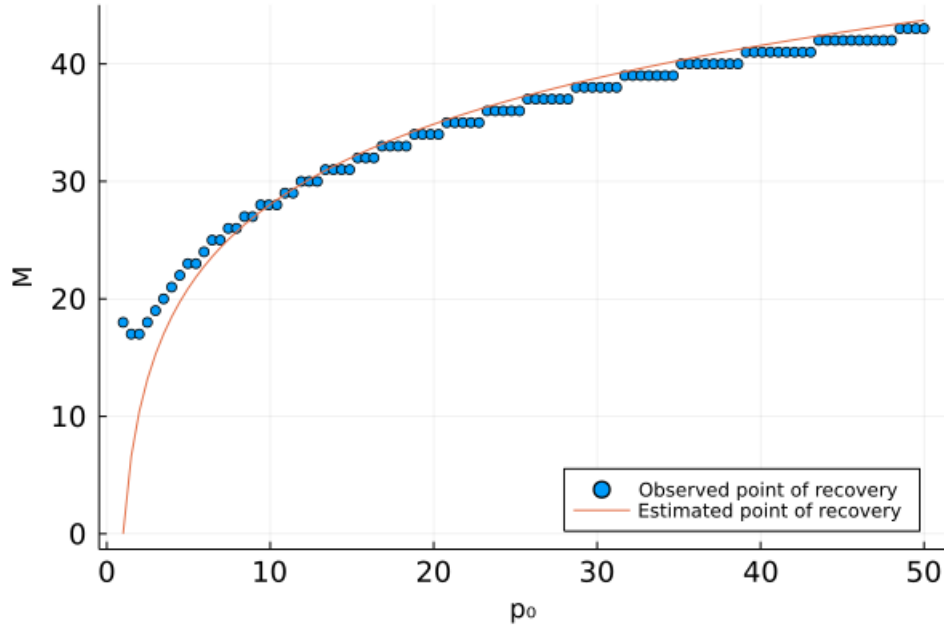


FIGURE 3.2. Observed resource recovery time (circles) and estimated recovery time using Equation 3.7 (solid line) in System 3.5 as a function of initial consumer density p_0 . In this figure, $\delta_p = 0.9$, $\gamma_p = 1$, $\sigma = 2.67$, $\delta_n = 0.8$, $\gamma_n = 1$, $R = 2$.

In figure 2 we show that Equation 3.7 is a reasonably close estimator of the observed point of recovery, especially for large values of the initial consumer density p_0 , where the consumer density is an order of magnitude higher than the initial resource density n_0 . We will show in the following theorem that the long term dynamics seen in Figure 1 did not depend on the initial conditions of the model.

THEOREM 3.3.2. *System 3.5 has a compact, connected global attractor in the first quadrant $M = \{(p, n) \in \mathbb{R}^2 : p \geq 0, n \geq 0\}$.*

See Appendix C for the proof of this theorem. Theorem 3.3.2 implies that, when $\gamma_p < \gamma_p^*$, System 3.5 will go towards carrying capacity of resource and extinction of consumers. On the other hand, when $\gamma_p > \gamma_p^*$, there are no stable fixed points in the first quadrant. Thus, Theorem 3.3.2 implies the existence of a nonlinear attractor, which we can describe based on numerical observations, as seen in Figure 3.

When $\gamma_p > \gamma_p^*$, the resource population is able to reach a maximum density of carrying capacity and stay there for a prolonged period of time (Figure 3). However, after the consumer reaches a

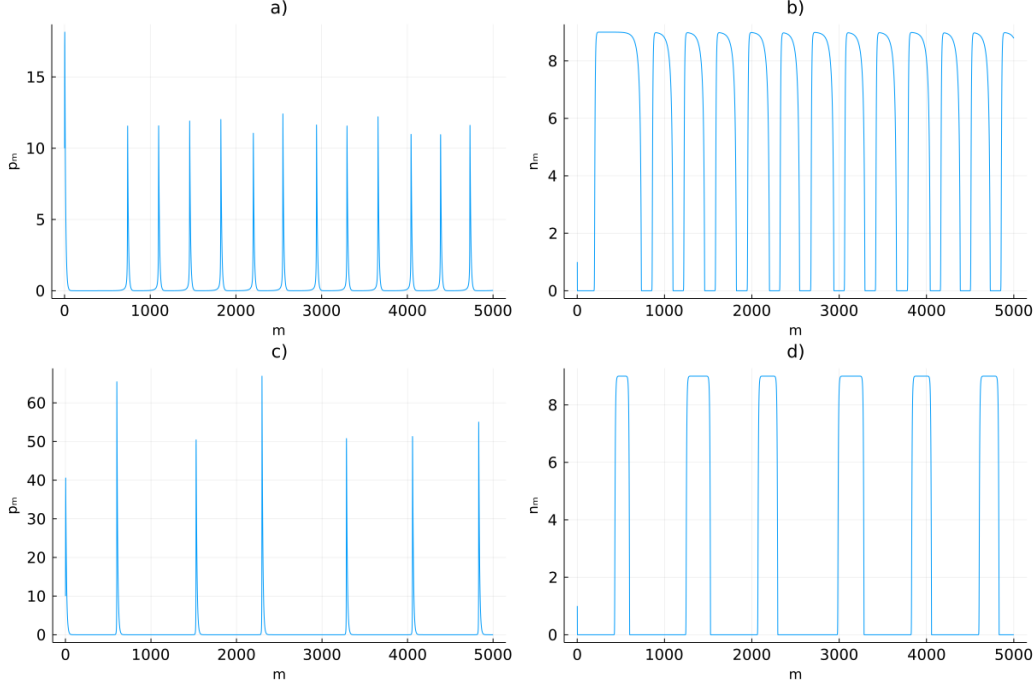


FIGURE 3.3. Time series of consumers p_m (**a** and **c**) and resource n_m (**b** and **d**) following System 3.5 for 5000 time steps (m). In this figure, $p_0 = 10, n_0 = 1, \delta_p = 0.9, \sigma = 2.67, \delta_n = 0.8, \gamma_n = 1, R = 2$, and the consumer conversion intensity $\gamma_p = 3$ (**a** and **b**) and $\gamma_p = 8$ (**c** and **d**).

high enough density, the resource population collapses and passes through a transient extinction phase. This cycle repeats itself through time, but at each repetition, the amplitude of consumer density varies. We hypothesize that this variation in amplitude is caused by the system having a long periodicity. In addition, increasing γ_p increases the period between each oscillation. This is consistent with the implication from Theorem 3.3.1 that a higher consumer density causes the resource to stay around the extinction equilibrium for a longer period of time.

Figure 3 also shows that the system can stay around the resource-only equilibrium for a prolonged time. We approximate this time in the following Theorem, proven in Appendix D.

THEOREM 3.3.3. *Let $\gamma_p > \gamma_p^*$, where γ_p^* is defined by Equation 3.6 and let*

$$(3.8) \quad \lambda_1 = \delta_p + \gamma_p \frac{n^*}{1 + \sigma n^{*2}}.$$

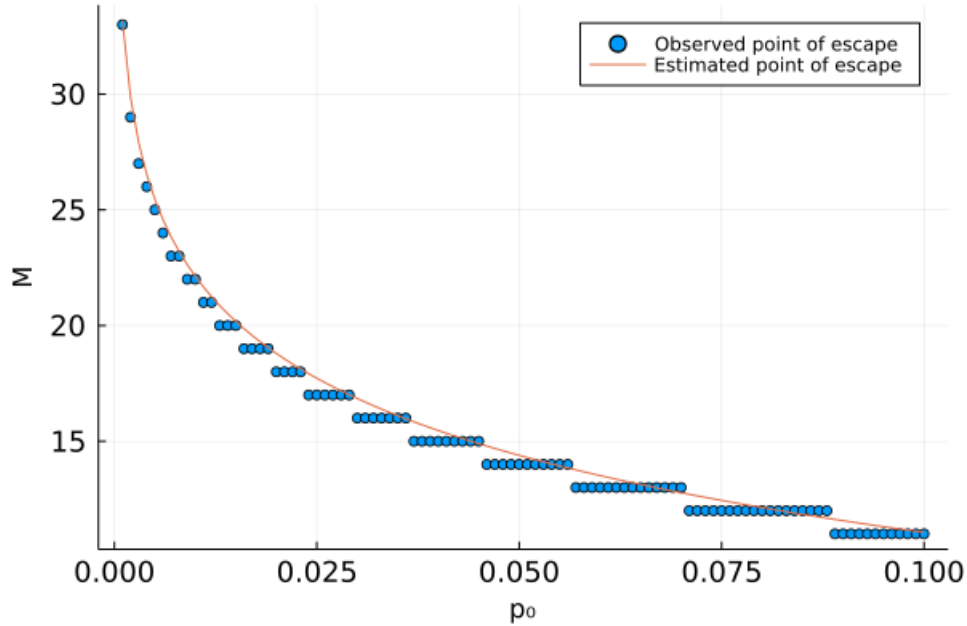


FIGURE 3.4. Observed escape time of consumer extinction (circles) and estimated recovery time using Equation 3.9 (solid line) in System 3.5 as a function of initial consumer density p_0 . In this figure, $\delta_p = 0.9, \gamma_p = 8, \sigma = 2.67, \delta_n = 0.8, \gamma_n = 1, R = 2$.

Then, if $(p_0, n_0) = (\varepsilon, n^* - \varepsilon)$ for $0 < \varepsilon \ll 1$, System 3.5 goes a crawl-by transient at the resource-only equilibrium $n = n^*$. resource will start decaying after a time of approximately

$$(3.9) \quad M = O\left(\frac{\log\left(\frac{1}{\varepsilon}\right)}{\log(\lambda_1)}\right).$$

In figure 4 we show that this expression is a reasonably close approximation of the time it takes for the consumer to escape extinction across a wide range of orders of magnitude for the initial consumer density.

3.3.2. Ghost attractors. Theorem 3.3.2 ensures that, when $\gamma_p < \gamma_p^*$, System 3.5 will converge to the stable equilibrium $(0, n^*)$. However, when $\gamma_p^* - \gamma_p \ll 1$, this convergence can take a significantly longer time, as can be seen in Figure 5. Before the system reaches the equilibrium, the dynamics resemble pseudo-oscillations similar to those observed in Figure 3 when $\gamma_p > \gamma_p^*$.

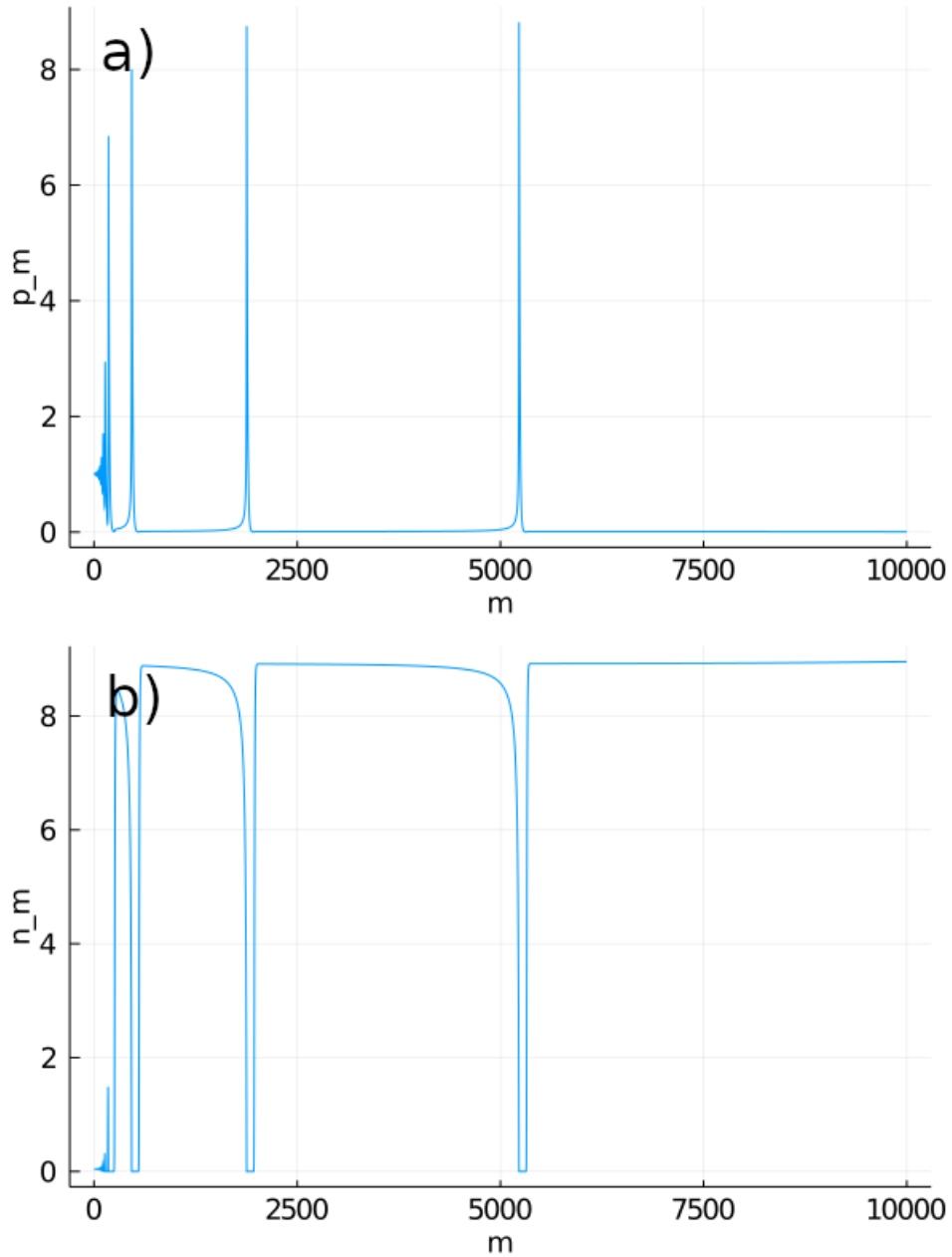


FIGURE 3.5. Time series of **a)** consumers p_m and **b)** resource n_m following System 3.5 for 10000 time steps. In this figure we consider $p_0 = 0.99p^\vee, n_0 = 1.01n^\vee, \delta_p = 0.9, \gamma_p = 0.9912\gamma_p^*, \sigma = 2.67, \delta_n = 0.8, \gamma_n = 1, R = 2$. Although we know that the system will converge to the equilibrium point, this convergence takes over 5000 time steps.

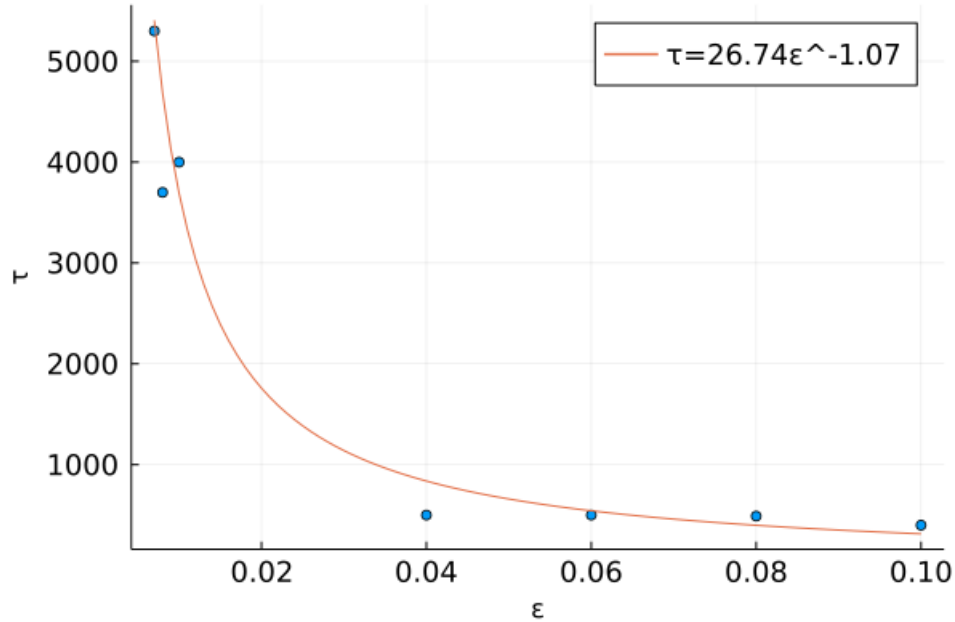


FIGURE 3.6. Approximation of transient time (τ) following Equation 3.10, where $\varepsilon = \gamma_p^* - \gamma_p$. In this figure, $p_0 = 10, n_0 = 1, \delta_p = 0.9, \sigma = 2.67, \delta_n = 0.8, \gamma_n = 1, R = 2$.

Given limitations of available analytical tools for exact derivation of limit cycles in discrete-time models, we approximate the time spent in the ghost attractor τ by considering a power law for the time spent in a limit cycle [98]:

$$(3.10) \quad \tau(\gamma_p) = A(\gamma_p^* - \gamma_p)^{-B}.$$

Whenever $n_M > n^\wedge$ and $p_M < p^\wedge$, System 3.5 shows that $n_{k+1} > n_k$ and $p_{k+1} < p_k$ for all $k > M$. Therefore, we identify the time the system escapes the ghost attractor as $\tau = \min\{M : n_M > n^\wedge, p_M < p^\wedge\}$. Figure 6 shows that this approximation using the power law provides a reasonable approximation.

3.4. Discussion

In this work we have identified two types of long transients, crawl-by transients and ghost attractors, that can appear in a consumer-resource system with group defense with discrete reproductive pulses. Our long-term dynamics are qualitatively different from those found in [29],

where they identified a variety of bifurcations and chaotic dynamics. The key differences between the two models are that, while that of [29] models reproduction as a continuous process and integrates the density-dependent growth for a case with overcompensation in discrete time, our model considers reproduction as a discrete event and has a saturating density-dependent function. The model in [29] is a discrete-time model similar to the Ricker model, where increased reproduction rates lead to unstable dynamics [116]. When modelling reproduction as a discrete process with saturating (Beverton-Holt style) density dependence rather than overcompensation, our analysis did not suggest that increased reproduction numbers leads to instabilities in our model.

In addition, discrete reproduction events are one of the main reasons we see the long transients analyzed in this model. The crawl-by transient observed at high consumer densities (Theorem 3.3.1) is caused by a sudden crash in the adults of the resource population, which is followed by a slow crash of the consumer population due to its inability to find enough resource for self-replacement. Although the adult resource population is almost nonexistent, the few remaining individuals eventually lead to an increase the resource population when the consumer population becomes small enough.

The other reason long transients appear in this model is due to the self-replacement of consumers depending on the ability of resource to defend themselves. The Type IV Holling functional response produces a bifurcation on the proportionality constant γ_p at the value γ_p^* given by Equation 3.6. This constant can be associated with the conversion capability of consumers, i.e. the amount of energy invested in reproduction activities. When the conversion capability of consumers is too small ($\gamma_p < \gamma_p^*$), group defense of resource will prevent self-replacement of consumers at high resource densities, which will lead to collapse of consumers. When this conversion capability is high enough, self-replacement can be satisfied, and the consumer-resource cycles of Figure 3 will occur. These cycles and their condition for existence resemble those found in other models where a mechanism of group defense of resource is considered [2, 134, 135].

In the case where the system presents consumer-resource cycles, the resource-dominated phase will include a crawl-by transient when the conversion capability is close to this bifurcation value (Theorem 3.3.3). This will follow by a crash of the resource population, where the consumer-dominated phase appears and presents the crawl-by transient previously described. This behavior

presents an alternative perspective to the concept of alternate stable states [10], where the different “alternative stable states” constitute long transients, which may resemble stable states during a long period of time, which then transition into the other phase and stay in a different long transient. In reality, stochasticity may render this juvenile survival when rare impossible or accelerate consumer death, which may lead the model to a stable state in a shorter period of time [113].

When the conversion capability of consumers is smaller than the critical value γ_p^* but close to it, these quasiperiodic orbits do not disappear completely and stay as ghost attractors. This ghost attractor stays until the resource density surpasses a given threshold (the equilibrium value n^\wedge) and the system enters the basin of attraction of the resource-only equilibrium. The emergence of this ghost attractor is caused by group defense, because in its absence ($\sigma = 0$), the unstable equilibria that cause the quasiperiodic orbits (p^\wedge, n^\wedge) do not exist. In their absence, resource population density will consistently increase and the consumer density decrease.

The estimation of the transient time of the ghost attractor shows one of the limitations of our analysis, as the theory to study limit cycles in discrete-time systems is not developed enough to precisely analyze the transient time of this ghost attractor. Given the seasonality of the reproduction and recruitment for many organisms [6, 19, 119, 138], a continuous-time model may not properly reflect the biological dynamics we are interested in. Despite this challenge, the expression for the transient time found for transient limit cycles in continuous-time systems in [98] is a reasonably accurate fit in our model. The transient times of the ghost attractor found in our work are similar to those found in the predator-prey model with group defense of [135]. However, our biological mechanisms differ, as their transients could be attributed to search time of prey from the predators through space, a feature not explicitly modelled in our work. In contrast, the length of the ghost attractor in our model can be attributed to the length of the crawl-by transients that are part of the cycle itself, which are periods of low population growth for either the consumer or the resource.

In conclusion, we show how long transients can appear in predator-prey systems with group defense and discrete recruitment pulses. A possible extension of this model is to explicitly consider the dynamics of the juvenile stages through a continuous-time model, which could give a more accurate approximation of the transient times found in this paper. A multi-stage model would also

allow exploration of the effect of relative adult versus juvenile vulnerability to consumption on the transient dynamics.

How far to build it before they come? Analyzing the use of the Field of Dreams hypothesis to bull kelp restoration

4.1. Introduction

One of the main challenges in restoration ecology is understanding the intensity and extent of the efforts required to achieve restoration goals [15]. The idea that partial restoration might be effective is embodied in the Field of Dreams hypothesis [107], which postulates that setting up favorable conditions for restoration at the beginning of the project can be enough to promote the natural processes that will lead to a successful restoration effort. Partial restoration has been successful in cases such as short-term habitat enhancement through a one-time coral reef transplantation, which then enhanced a longer-term natural recovery of coral [96], or reintroduction of former native species in degraded systems, which leads to increases in species richness in the community [114]. However, partial restoration may not always be effective at achieving management goals. In some cases the resulting community may not be desirable due to a lower diversity than the target community [146], or stochasticity may bring similar ecosystems to completely different states, making further restoration efforts necessary if one of the states is undesirable [131].

These examples raise the question of under what conditions engaging in partial restoration efforts and then relying on natural processes for ecosystem recovery can achieve restoration goals. This question can be explored in terms of partial restoration efforts occurring at three different scales [1, 143]. First, considering the spatial scale, partial restoration depends on the extent of the restoration effort that will then lead to natural recovery of the rest of the region through spread. Second, considering the temporal scale, partial restoration arises from performing restoration efforts at a short-term timeframe and longer term recovery following from natural dynamics. Third, considering the ecological scale, partial restoration arises from targeting a species or component of the community (e.g. reintroducing a foundational or early successional species, or removing a pest

species), and then recovery of additional species in the community occurs naturally (e.g. through succession). Existing evaluations of partial restoration have explored different scales. For example, [127] tested the ecological scale of restoration in terms of whether restoring dune vegetation could lead to the natural recovery of beach mice. They found that beach mice occupied restored habitats almost as frequently as natural habitats. In addition, a meta-analysis by [72] of seagrass restoration found that as the spatial scale increases, the likelihood of restoration success increases as well. Therefore, different aspects of partial restoration might vary in their efficacy, and a next step in understanding the efficacy of a Field of Dreams approach is to comprehensively evaluate the interaction between all three scales of partial restoration: spatial, temporal, and ecological.

Resolving the effect of these different scales on restoration success is particularly relevant to systems with the potential for alternative stable states and threshold dynamics. If an ecological system exhibits multiple stable states for a single set of environmental conditions, disturbance can lead to a shift in the system to an undesirable state or ecosystem function with impeded recovery [10]. In this case, the unstable threshold represents a target restoration must cross for recovery to occur [128]. In the context of the Field of Dreams hypothesis, such a threshold can provide specific partial restoration goals that have to be fulfilled before natural recovery is possible. While the potential for alternative stable states has been identified across terrestrial [64, 110] and marine [24, 101, 123] systems (further reviewed in [42]), establishing whether such states represent prohibited versus slowed recovery is difficult to resolve empirically given challenges over resolving community outcomes at large temporal and spatial scales [109].

A system that exemplifies these multi-faceted components of partial restoration is temperate rocky reefs. Temperate rocky reefs have experienced kelp declines and associated increases in kelp-grazing urchins in several parts of the world [76], including southern Australia [81] and northern California [118], motivating novel restoration initiatives [100]. In addition, temperate rocky reefs can exist in kelp forest or urchin barren states, which might represent alternative stable states depending on an array of nonlinear feedbacks [87]. For example, urchins typically subsist off of kelp blades that detach from extant kelp and drift into the seafloor (“drift kelp”), such that grazing does not cause kelp mortality, especially when predator presence induces cryptic urchin behavior [55]. However, at low kelp densities, which might arise from environmental disturbances

such as heat stress, low nutrients, or storms [11], urchin starvation and low predator density can lead to more active kelp grazing, which further increases kelp mortality [55]. In this sense, outcomes in kelp forests likely arise from a mix of bottom-up and top-down processes [50, 70, 97]. Urchins in urchin-dominated barrens can go dormant for prolonged periods of time and at high densities that limit the capacity for kelp to settle. This has led restoration efforts to focus on urchin removal [83, 140]. However, the spatial and temporal extent of urchin removal necessary for kelp recovery is uncertain, and several strategies that extend the ecological scale of restoration, such as kelp reseeding (introducing kelp seeds or juvenile stipes) and outplanting (planting mature kelp stipes), are under exploration [40, 100].

For example, the Sonoma and Mendocino County coastlines of northern California experienced a 95% decline in bull kelp (*Nereocystis luetkeana*) forest coverage [97]. These declines occurred due to multiple factors including anomalously warm seawater temperatures between 2014-2016 and nutrient-poor water, that stress kelp and increase purple urchin (*Strongylocentrotus purpuratus*) recruitment [97, 118], and the local extinction of the sunflower sea star (*Pycnopodia helianthoides*), the main natural predator of urchins in this region, due to the sea star wasting disease outbreak in 2013 [56]. This decline in kelp coverage has led to the starvation of other herbivores, which has resulted in the closure of the recreational red abalone (*Haliotis rufescens*) fishery and the decline of the commercial red sea urchin (*Mesocentrotus franciscanus*) fishery [118]. This economic impact has accentuated the demand to restore the kelp forest ecosystems in this region. Proposed restoration strategies include urchin removal, kelp reseeding, and outplanting [61]. The novelty of these restoration efforts provides high uncertainty on what impact might they have and how they will influence the spatiotemporal patterns of purple urchin density.

In this paper, we use a dynamical population model to explore how the spatial, temporal, and ecological scales of restoration extent influence restoration efficacy in the context of bull kelp restoration in the northern California temperate rocky reefs. To do this, we analyze two metrics for restoration efficacy: the threshold urchin density for natural kelp recovery and the rate of kelp recovery. We evaluate the spatial scale by exploring how varying the portion of the intervened coastline by restoration influences these metrics. We explore the temporal scale by applying the intervention either just at the beginning of the restoration project or through continuous efforts.

Finally, we explore the ecological scale by analyzing how reintroducing kelp or reducing urchin density, separately and in combination, influences these metrics.

4.2. Methods

4.2.1. Model overview. In this subsection we present an overview of the model we use to describe the spread dynamics of kelp, and in the following subsection we provide a mathematical formulation of the model. This model follows the distribution of kelp and urchin populations through survival, reproduction, and dispersal over a one-dimensional coastline (Figure 4.1).

At each time step the adults survive with a given probability. We assume that urchin survival is density independent. Kelp survival depends on the grazing intensity by urchins, which depends on both urchin and kelp density. Direct grazing intensity is unimodal with kelp, at first increasing with resource availability and then decreasing at high kelp densities, as might occur due to a switch from active grazing to passive subsistence off of drift kelp [55]. Adult kelp produces spores at a constant per capita amount, whereas urchins larvae production depends on kelp grazing and drift kelp consumption. Spores and larvae then disperse through the coastline and a fraction of them settle and become adults. In line with observations of urchin adult movement on the scale of a few meters [36], kelp seeds and zoospore movement on the scale of tens of meters [32], and urchin larval movement on the scale of kilometers [80], we assume that adult urchin movement is significantly smaller than dispersal of the kelp and urchin juvenile stages, and thus neglect any adult urchin movement.

We vary the amount of urchin removal, kelp reseeding, and kelp reintroduction over a range of spatial and temporal extents. We focus on these interventions, and do not include predator reintroduction as well, for two reasons. First, research into the feasibility of seastar reintroduction as a restoration intervention for our focal system of the California north coast is still in development and at the stage of lab tests (J. Hodin, personal communication), while urchin removal is underway [139] and kelp reseeding and reintroduction are undergoing field tests (B. Hughes, personal communication). Therefore, this focus centers our analysis on established and ongoing management approaches and decisions. Second, an open question under current investigation for the feasibility of predator reintroduction is whether or not predators require non-barren urchins (i.e. urchins

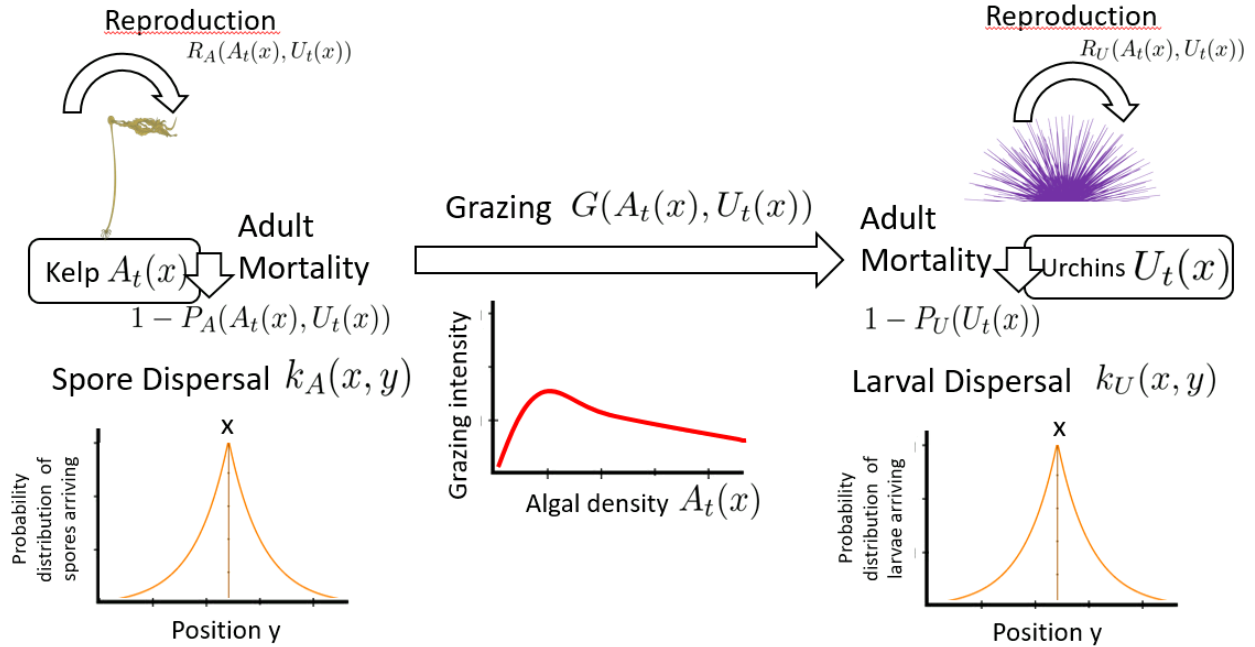


FIGURE 4.1. Overview of the dynamics of the model with the respective functional forms of the spore dispersal and grazing intensity. At each time step, a proportion of adults of each species dies off and recruits are produced and dispersed. The grazing interaction affects the spore production of urchins and kelp mortality. Diagram images thanks to Janes Thomas, IAN Image Library (<https://ian.umces.edu/imagelibrary/>)

in recovered kelp stands with enough kelp consumption to support gonad production) in order to consume and gain nutritional value from predation and therefore be viable after reintroduction (J. Hodin, personal communication). If so, then the interventions modeled here might be necessary first steps that precede any predator reintroduction, where our questions of the roles of different aspects of reintroduction scales can inform the efficacy of different approaches to these necessary first steps.

4.2.2. Model. Our model combines the ecological dynamics of [70] with the spatial dynamics of [68]. We consider populations of kelp and urchins cohabit in a one-dimensional coastline Ω . Our model follows kelp ($A_t(x)$) and urchins ($U_t(x)$) through time t and space x . At each time step and for each species i ($i = A$ for kelp and $i = U$ for urchins), the adults survive to the next step following the function $P_i(A_t(x), U_t(x))$ and adults produce recruits according to a function $R_i(A_t(x), U_t(x))$.

The recruit survive to the next step following a function $S_i(A_t(x), U_t(x))$ and disperse from their source following a kernel k_i in an integrodifference equation framework. Combining these dynamics, the populations for algae and kelp at the next time step follow:

$$(4.1) \quad \begin{aligned} A_{t+1}(x) &= P_A(A_t(x), U_t(x)) + S_A(A_t(x), U_t(x)) \int_{\Omega} k_A(x, y) R_A(A_t(y), U_t(y)) dy \\ U_{t+1}(x) &= P_U(A_t(x), U_t(x)) + S_U(A_t(x), U_t(x)) \int_{\Omega} k_U(x, y) R_U(A_t(y), U_t(y)) dy. \end{aligned}$$

Adult kelp has a natural survival probability in absence of urchin grazing given by δ_A , which implies a mean lifespan of $1/\delta_A$. In addition, kelp survival depends on urchin grazing, which we model as a Holling's "Type IV" functional response $G(A_t(x), U_t(x))$. This functional response phenomenologically represents a behavioral shift from active to passive grazing with increasing kelp and can lead to two alternate stable states: a kelp-dominated state (kelp forest) and an urchin-dominated state (urchin barren) [70], which occurs under our parameterization (Appendix E). Urchins graze kelp holdfast with a base attack intensity γ_A . Given a maximum grazing consumption at $A_t(x) = \frac{1}{\sqrt{\sigma_A}}$, adult kelp survival is:

$$(4.2) \quad P_A(A_t(x), U_t(x)) = \delta_A A_t(x) \max(1 - \gamma_A G(A_t(x), U_t(x)), 0)$$

$$(4.3) \quad G(A_t(x), U_t(x)) = \frac{U_t(x) A_t(x)}{1 + \sigma_A A_t(x)^2}.$$

We assume that kelp produces a constant per capita number of spores R , which gives $R_A(A_t(y), U_t(y)) = R A_t(y)$. Kelp spore survival and recruitment depends on two factors: the probability of spores settlement and urchin predation. Settlement is density-dependent with a saturating, Beverton-Holt-type function given the maximum kelp population at a given location x of $\frac{1}{\beta}$. In addition, we assume that urchins graze recently settled kelp stipes before they can grow to a mature sporophyte with a per capita probability γ_S . Then, the survival of kelp spores is

$$(4.4) \quad S_A(A_t(x), U_t(x)) = \frac{\max(1 - \gamma_S U_t(x), 0)}{1 + \beta A_t(x)}.$$

Urchin survival occurs with a constant probability δ_U , which gives us $P_U(A_t(x), U_t(x)) = \delta_U U_t(x)$. Urchin larval production arises from two sources. First, urchins gain energy through direct grazing, proportional to Equation 4.3 with a proportion constant γ_U [103]. Second, urchins gain energy for larval production through drift kelp consumption at a constant proportion ε of the kelp available at each location x . Both γ_U and ε encapsulate conversion of energy gained from kelp consumption into larval production and survival such that $S_U(A_t(x), U_t(x)) = 1$. Combining both sources of energetic gain, the total urchin larval production is

$$(4.5) \quad R_U(A_t(y), U_t(y)) = \gamma_U G(A_t(y), U_t(y)) + \varepsilon A_t(y) U_t(y).$$

Finally, we model both dispersal kernels as Laplace kernels with mean dispersal distance for each species i $1/a_i$ given by the equation [88]:

$$(4.6) \quad k_i(x, y) = \frac{a_i}{2} \exp(-a_i|x - y|).$$

Note that, with constant and homogeneous kelp natural mortality δ_A , kelp spore production R , and urchin production γ_U and ε , we focus on kelp-urchin interactions and ignore the role of seasonal and variable environmental conditions in driving kelp and urchin dynamics. We make this simplifying assumption because of our focus on restoration decisions concerning the choice of urchin removal and kelp reintroduction interventions at different spatial extents and temporal scales. Informing the additional (and important) restoration decisions of optimal location and timing of restoration interventions, not under consideration here, would require model extensions that account for spatially heterogeneous and temporally stochastic environmental drivers such as nutrients, light, and wave disturbance that can influence kelp dynamics [50, 70], as well as the stochasticity and seasonality of urchin reproduction [23, 106].

4.2.3. Parameter estimation. We fit the model without interventions to kelp and urchin distribution data in the Sonoma-Mendocino coast. We compile yearly kelp coverage data from the dataset of [97] with the yearly urchin data of Reef Check [111]. We estimate all parameters except

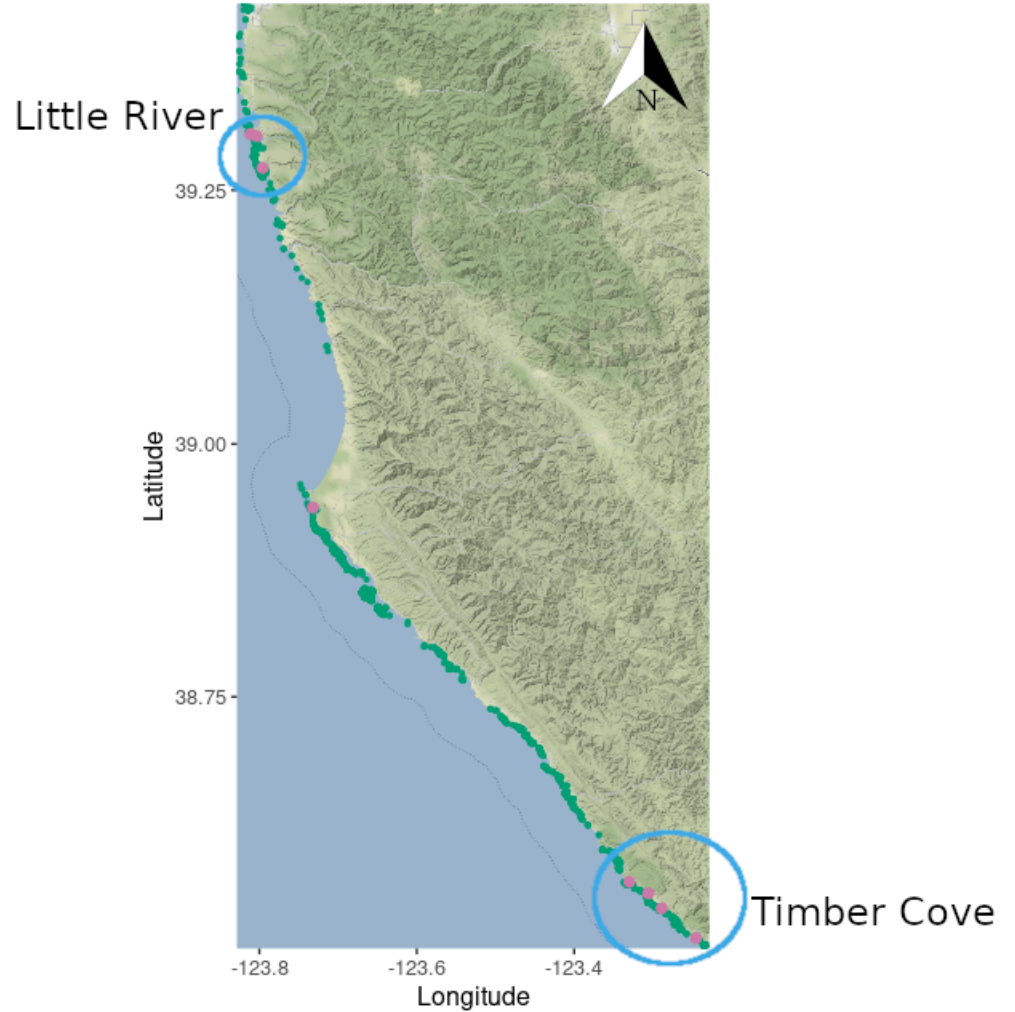


FIGURE 4.2. Kelp (green dots) and urchin (purple dots) data available for 2007-2008 in the Sonoma and Mendocino counties of California. Notice the highlighted regions, circled in blue, where urchin data is available. These regions correspond to Little River (top circle) and Timber Cove (bottom circle). Notice the purple dot in the middle of the map corresponds to a single spatial point, which makes our spatial analysis unfeasible.

β using the 2007 and 2008 data (Figure 4.2). We identify two regions with available urchin data, which correspond to the coasts of Little River and Timber Cove.

We estimate the parameters using the Approximate Bayesian Computation (ABC) method, implemented using the EasyABC package in R [63]. In order to reduce estimation errors due to possible parameters correlations, we will implement the ABC algorithm with Metropolis-Hastings sampling, implemented in the EasyABC package as the Marjoram method and described in [141].

Using the ABC algorithm, we start our simulations taking the initial conditions $A_0(x), U_0(x)$ being the distribution for each of the regions at the 2007 measurement. We initialize our ABC algorithm with uniform prior distributions for each of the parameters in the range presented in Table 4.1. We then run the model for a sampled combination of parameters for a year (where each time step t corresponds to 1 month) and compare the obtained kelp distribution $A_{12}(x)$ with the distribution at the 2008 measurement. We compare these distributions through using RMSE as our summary function. In other words, if $A_{12}(x)$ is the 2008 distribution in the given region, we find combinations of parameters that minimize:

$$\text{RMSE} = \left(\int_{\Omega} (A(x) - A_{12}(x))^2 dx \right)^{1/2}.$$

While this approach ignores the seasonal nature of kelp and urchin recruitment as well as kelp mortality from winter storms [38, 126], in the absence of monthly data that would allow model-fitting to seasonal processes, it does capture the year-to-year dynamics that match the time scale of the data.

To estimate the β parameter that inversely determines the kelp recruitment saturation level, we perform a linear regression at each point in space in the kelp distributions from 2004 to 2009 and fit it to a Beverton-Holt model [12]. This procedure allows us to make use of the higher availability of kelp data, and reduce the number of parameters our ABC procedure has to estimate. We then use the distribution of maximum densities as our distribution for $\frac{1}{\beta}$.

4.2.4. Control strategies and model analysis. To explore what control strategies promote the spread of kelp, we follow the restoration focus of the Sonoma-Mendocino Bull Kelp Recovery Plan [61]. This Recovery Plan focuses in implementing several restoration strategies near kelp “oases”, i.e. patches of extant kelp, to try to enhance kelp expansion to nearby regions. We explore three restoration strategies around these oases: urchin removal, kelp re-seeding, and kelp outplanting.

We initialize our simulation with initial condition of kelp $A_0(x)$ be 0 everywhere except at a starting oasis of length L , in which we start with kelp at an initial kelp density A_0 ; the urchins initial density is U_0 throughout the coastlines Ω . To identify target restoration locations as kelp

density (and therefore the location of oases) changes through time, at each time step t , we define the region where restoration efforts are applied as the set of all locations centered around x with length η where the kelp density surpasses a critical density A_c . This gives us a function $\delta_t(x)$ to indicate the presence or absence of restoration actions given by

$$(4.7) \quad \delta(x) = \begin{cases} 1 & \text{if } \int_{x-\eta/2}^{x+\eta/2} A_t(y) dy \geq A_c, \\ 0 & \text{otherwise.} \end{cases}$$

Multiplying implementation presence $\delta_t(x)$ by the control intensity of urchin removal μ_U , kelp seeding μ_S , or kelp outplanting μ_A , provides the terms for modifying the survival probability of adult urchins, spore production of kelp, and survival probability, respectively, when implementing restoration, yielding

$$(4.8) \quad P_U(U_t(x)) = \gamma_U(1 - \mu_U\delta(x))U_t(x),$$

$$(4.9) \quad R_A(A_t(x)) = R(1 + \mu_S\delta(x))A_t(x),$$

$$(4.10) \quad P_A(A_t(x), U_t(x)) = \delta_A A_t(x) \left(1 + \mu_A\delta(x) - \gamma_A U_t(x) \frac{A_t(x)}{1 + \sigma_A A_t(x)^2} \right).$$

We explore the temporal scale of restoration through two scenarios: first we implement a short time scale restoration effort by varying the initial densities A_0 and U_0 and setting long-term control $\mu_i = 0$ for function $i = U, S, A$. This corresponds to the case in which partial restoration efforts are performed at the start of the project, and then natural processes (e.g. succession) might eventually achieve restoration goals. Second, we implement a long time scale restoration effort where the initial kelp and urchin densities A_0 and U_0 are fixed, and we vary the restoration effort intensity μ_i . For these simulations, we set the initial kelp density $A_0 = 1/\beta$ within the oasis (and zero elsewhere) and initial urchin density U_0 to 95% of the threshold value that the system must cross for kelp recovery. Then, for ongoing restoration intervention, we explore a range of intensities in terms of a percentage increase in urchin mortality (urchin removal), kelp spores (seed outplanting), and adult

kelp (kelp outplanting). In each case we explore weak (10%), moderate (40%), and strong (70%) intensities.

In both temporal scale scenarios, we explore the effect of different spatial scales. For the short time scale scenario, we explore the spatial scale of restoration by varying the length of the initial oasis L . In the long time scale scenario, we explore the spatial scale of restoration by varying the size of the region with a control effort η . Finally, we explore the ecological scale of restoration by comparing scenarios with only a single control strategy or a combination of strategies (urchin removal, kelp re-seeding, or kelp outplanting) at varying intensities.

We evaluate these scenarios using two metrics. Our first metric is the maximum initial urchin density at which kelp can spread (hereafter the urchin threshold), which represents the restoration effort necessary for eventual recovery to take place. The second metric is the kelp recovery rate (hereafter spread rate). To calculate the spread rate, we run the system for 12 time steps (months) and, at each time step, calculate spread extent as the distance from the starting point $x = 0$ to the point x where there is a significant amount of kelp coverage is more than 1% of kelp coverage. We then calculate the spread rate as the slope of the linear regression of spread extent versus time. We choose months as our time scale to explore the dynamics of our system through the span of a single year, which allows us to see the short-term effect of the different restoration strategies, while also accounting for the annual nature of bull kelp, where factors not modelled, such as storm disturbance, might further affect kelp survival at the end of our time horizon.

In order to quantify the relative effect of different processes and management levers on the urchin threshold and spread rate, we perform a global sensitivity analysis of all parameters in the model, based on the procedure by [54]. We first sample 2000 combinations of parameters from the posterior distributions obtained from the parameter estimations and calculate the urchin thresholds and spread rates for each combination. We then construct a random forest using the R package `randomForest` [85], with the parameters of our model as predictors and the urchin threshold or spread rate as the target function. The `randomForest` package provides an importance metric for each predictor, which indicates how frequently that predictor served a breakpoint in the random trees of the forest.

4.3. Results

In our model parameterization, the ABC presented high uncertainty in all of the estimated parameters; we focus on our global sensitivity analysis influence of the different parameters on the model outcomes. We only show the results for the parameter estimates of the Timber Cove region, using the best-fit values presented in Table 4.1. We do this because the ABC of Timber Cove provided better posterior distributions than that of Little River, and thus less uncertainty. See Appendix F for the posterior distributions for both regions.

4.3.1. Urchin threshold. Given a short-term, one-time urchin removal, the threshold urchin density necessary for kelp recovery increases if, in addition to urchin removal, further kelp is planted (Figure 4.3). This occurs because increasing kelp density lowers the grazing intensity of urchins due to the behavioral feedback in the Type IV functional response of urchin grazing. Accordingly, an increase in σ_A (the parameter which determines the strength of the behavioral feedback) increases the threshold urchin density for kelp recovery. In the context of the Field of Dreams hypothesis, kelp natural recovery can be feasible after removing urchins below a certain threshold. Increasing the ecological scale of restoration through including kelp outplanting (i.e., increasing initial kelp density) increases this threshold, which reduces the intensity of urchin removal efforts required to ensure kelp recovery.

Our global sensitivity analysis (Figure 4.4) confirms the main factor that affects this threshold urchin density for kelp recovery is the urchin grazing activity (described by the conversion of kelp to urchins γ_A and the kelp grazing inhibition parameter σ_A). Specifically, the threshold urchin density is greater for slower urchin grazing (lower γ_A) and a lower peak value for direct kelp grazing (lower σ_A). In addition, the threshold urchin density is higher for a higher urchin natural mortality rate (lower urchin survival probability δ_U), higher initial kelp density (higher initial kelp density A_0), and with a lower kelp natural mortality (higher kelp survival probability δ_A).

4.3.2. Kelp spread rate. Given an initial urchin removal below the threshold value required for recovery, kelp spread rate increases with expanding interventions across ecological scales more than expanding over spatial or temporal scales. Under our baseline parameterization, ongoing kelp seeding enhances kelp recovery rate, while long-term, ongoing kelp outplanting or urchin removal

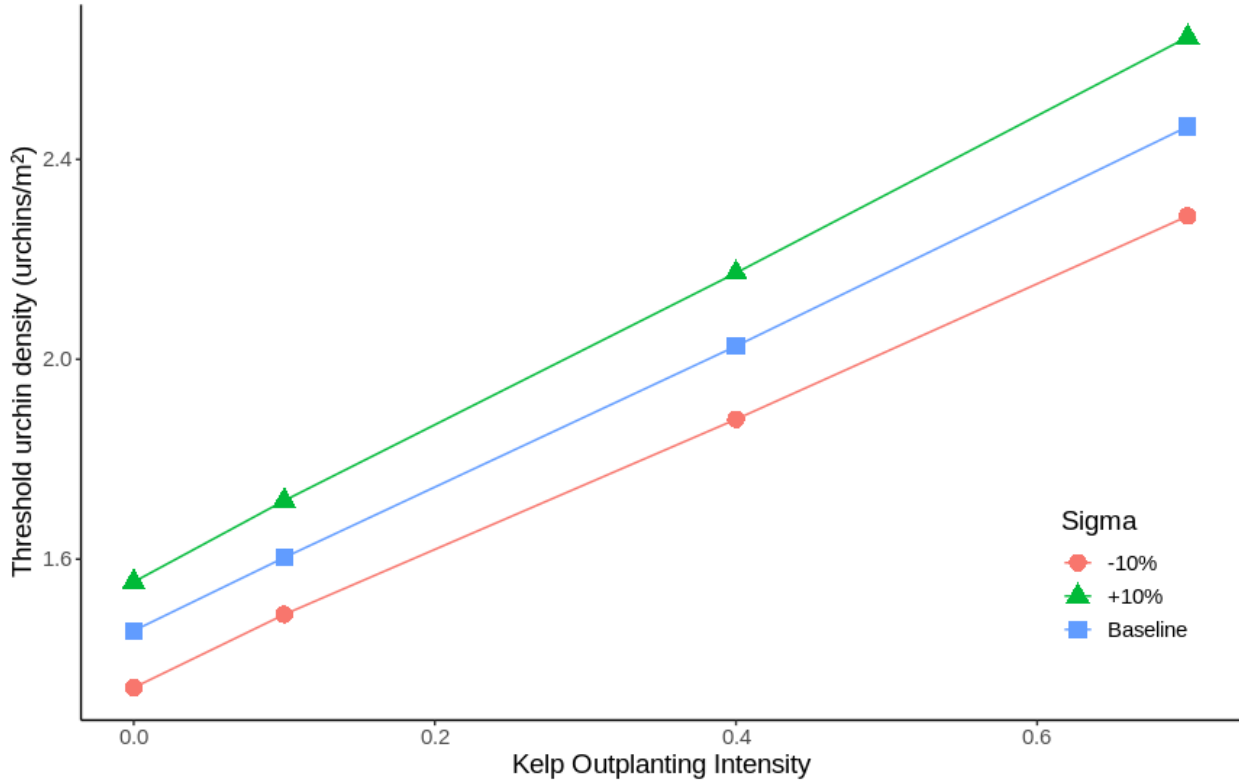


FIGURE 4.3. The threshold urchin density necessary for kelp recovery as a function of kelp outplanting intensity. Different lines represent different values of σ_A (inversely determines the kelp density of maximum urchin grazing in the Type IV functional response) changed by 10% from its baseline value.

do not (Figure 4.5). However, the relative effect of other strategies is sensitive to initial kelp density. With double the initial kelp density, further kelp outplanting increases kelp recovery rate (Figure 4.6a), while with triple the initial kelp density, ongoing urchin removal has a bigger effect on kelp recovery rate (Figure 4.6b). The greater sensitivity to initial kelp density for ongoing urchin removal and kelp outplanting, as compared to kelp reseeding, is likely due to the nonlinear (Type IV) feedback between urchin grazing and extant kelp as compared to the linear (Type I) feedback between urchin grazing and kelp seeds. These different dynamics lead to a different influence of the control strategies that directly affect the local kelp-urchin interaction.

For the spatial scale of restoration, increasing the extent of ongoing restoration efforts does not affect the rate of recovery of kelp (compare panels a) and b) of Figure 4.5). This suggests that kelp recovery is mainly determined by the local urchin grazing intensity, and extending restoration

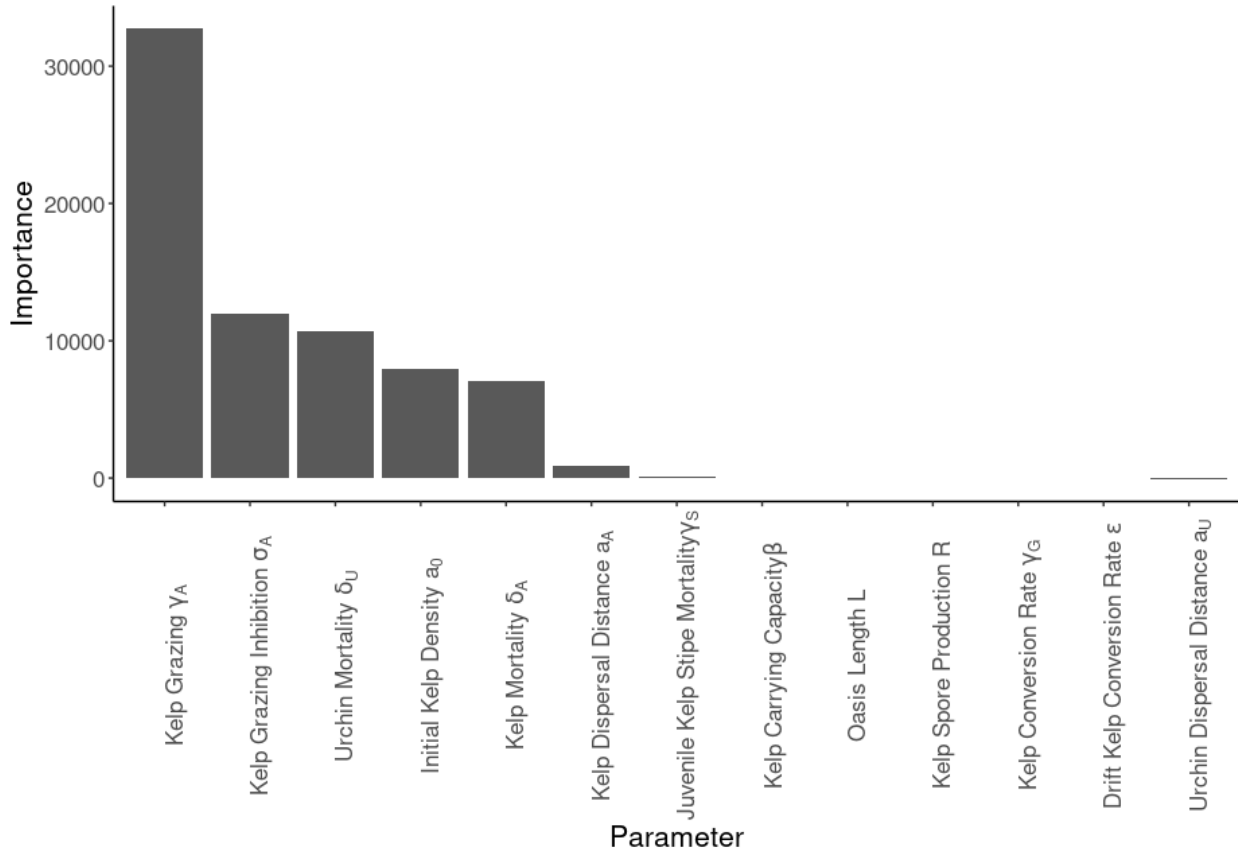


FIGURE 4.4. Importance ranking of the parameters of the Model 4.1 from the global sensitivity analysis of the threshold urchin density necessary for kelp recovery. See Table 4.1 for more detailed parameter definitions.

efforts to regions of the coastline with reduced kelp densities, where urchin grazing is stronger, will not affect kelp recovery rate. For the temporal scale of restoration, increasing the initial kelp density and decreasing the initial urchin density through a more intense partial restoration effort at the beginning enhance kelp recovery more than ongoing restoration efforts (compare the spread rates in Figure 4.7 to those in Figures 4.5 and 4.6). Increasing kelp density and reducing urchin density near the kelp oasis provides better conditions for kelp survival when interacting with the urchins, which further enhances kelp recovery rate. Overall, the combination of increasing initial kelp density, reducing initial urchin density, and implementing an ongoing kelp seeding leads to the fastest kelp recovery.

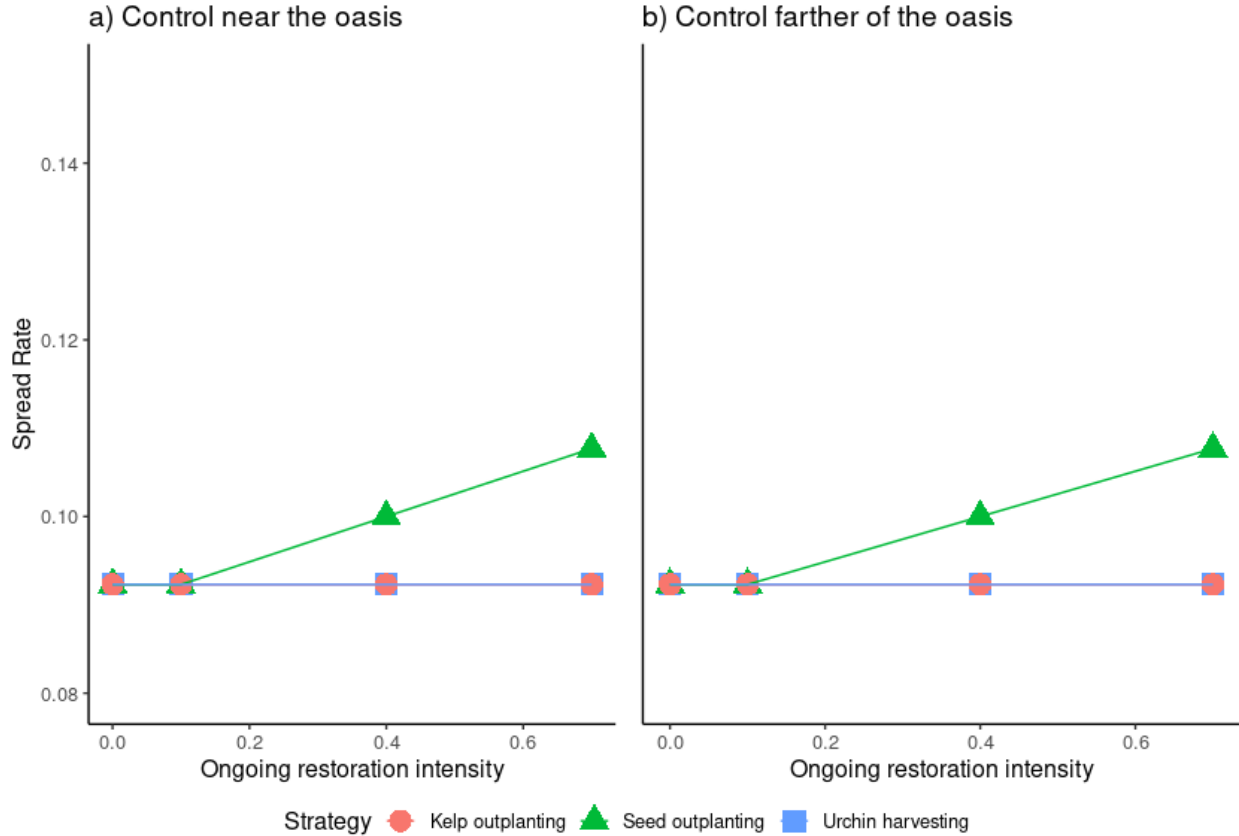


FIGURE 4.5. Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below the threshold value necessary for kelp recovery and with an initial kelp density $1/\beta$. Each line represents a different strategy: kelp outplanting in red circles, kelp seeding in green triangles, and sustained urchin harvest in blue squares. Panel a) shows ongoing restoration efforts near the kelp oasis ($\eta = 1$), and panel b) shows ongoing restoration efforts across a wider region of the coastline ($\eta = 10$).

The primary role of short-term restoration efforts is further evident in the global sensitivity analysis of the spread rate (Figure 4.8), where initial kelp and urchin densities (A_0 and U_0 respectively) have a higher impact over the spread rate than ongoing restoration efforts (μ_i for $i = U, A, S$). Therefore, both natural local conditions that lead to higher kelp coverage and lower urchin densities after a marine heatwave, as well as interventions to increase kelp density and decrease urchin density, have a strong impact on overall spread rate. When comparing the importance of the parameters for the threshold urchin density (Figure 4.4) and kelp recovery rate (Figure 4.8), we observe that parameters such as size of the oasis (L) and mean dispersal distance of kelp (a_A)

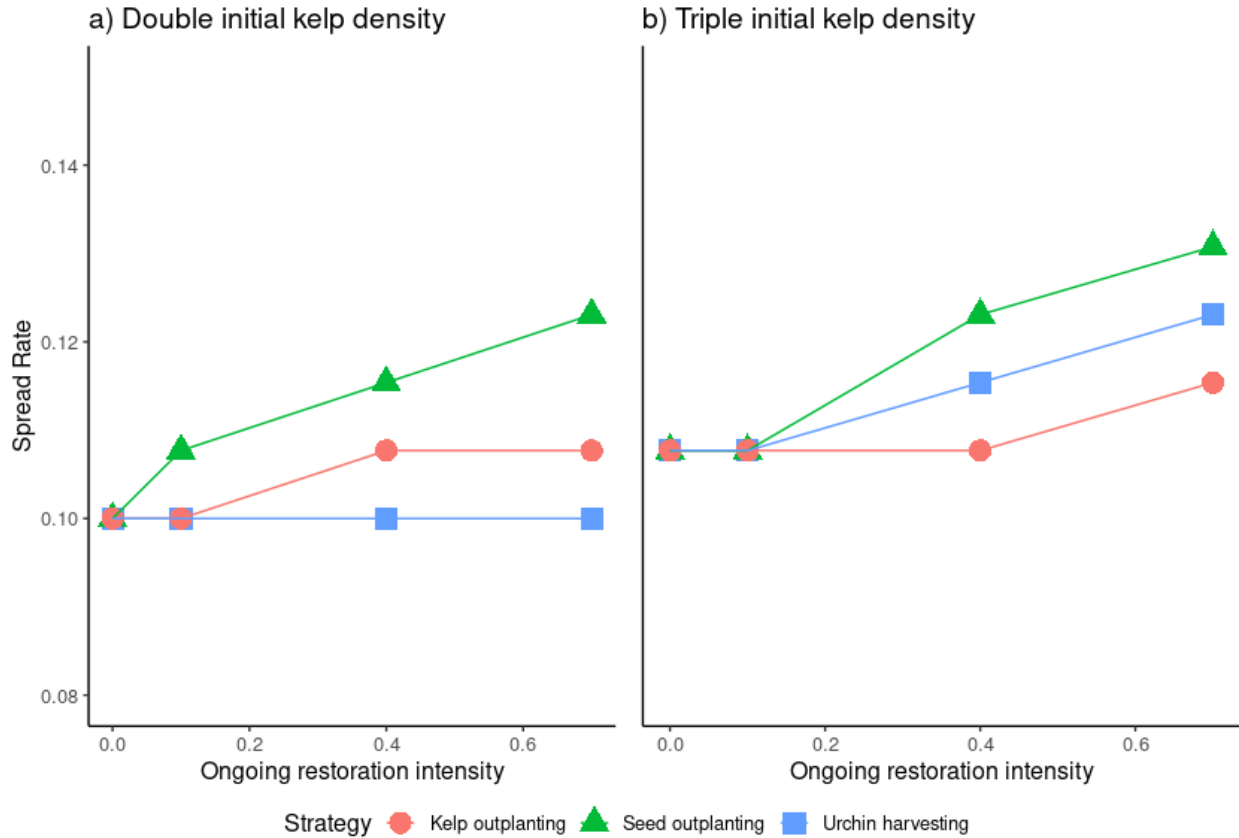


FIGURE 4.6. Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below the threshold value necessary for kelp recovery with a varying initial kelp density. Each line represents a different strategy: kelp outplanting in red circles, kelp seeding in green triangles, and sustained urchin harvest in blue squares. Panel a) shows ongoing restoration efforts with double the initial kelp density in the oasis compared to the default of $1/\beta$, and panel b) shows ongoing restoration efforts with triple the initial kelp density.

play a role on kelp recovery once urchin density is below the threshold necessary for recovery. Intuitively, a higher mean dispersal distance of kelp seeds (a_A) leads to a faster spread (Figures G.1-G.3 in Appendix G), especially for the strategy of seed outplanting. However, note that the relative efficacy of the different restoration strategies remain unchanged for different values of mean dispersal distances of kelp seeds. In addition, the lower importance value of kelp dispersal distance compared to parameters related to urchin grazing indicates that local kelp-urchin interactions have a greater influence on kelp spread rate than kelp dispersal. While increasing the size of the initial

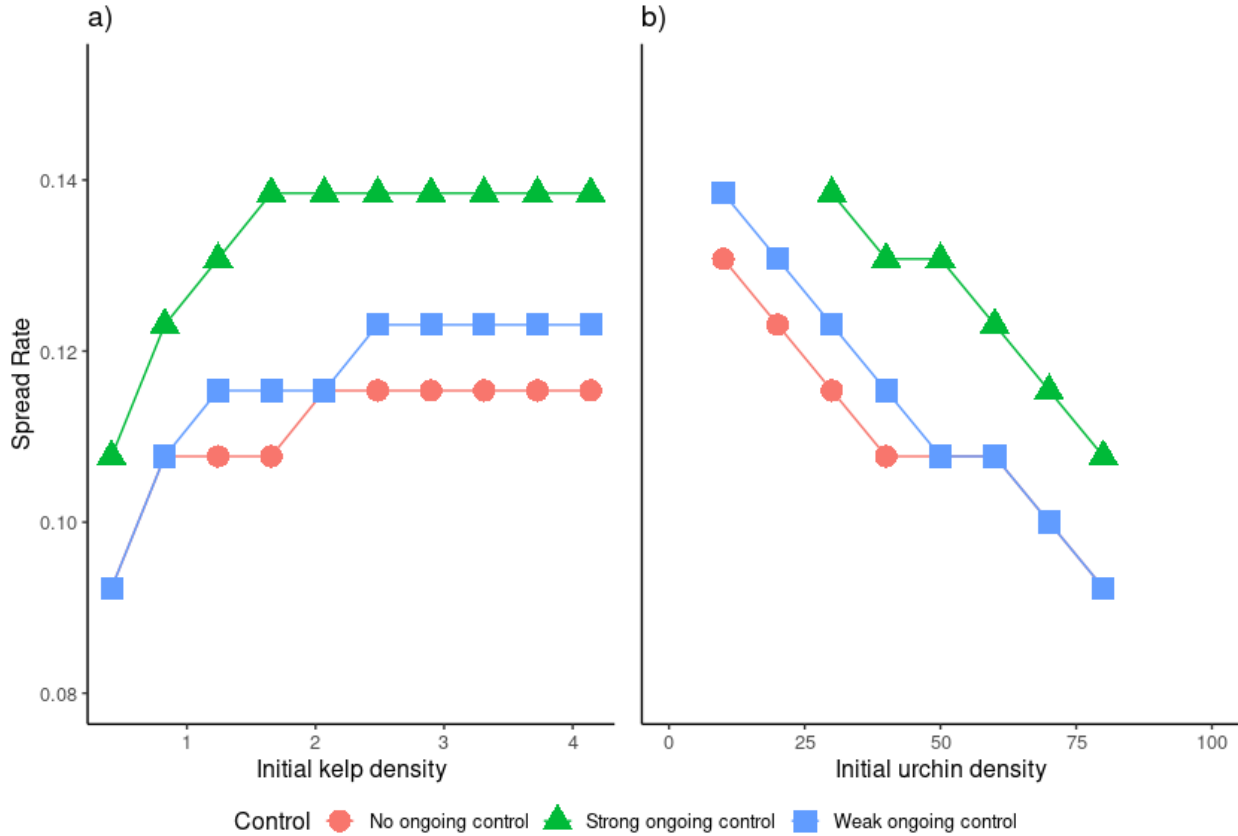


FIGURE 4.7. Kelp spread rate under different initial conditions for partial restoration efforts at the initial (short-term) restoration stage. Each line represents a different ongoing restoration effort in terms of kelp seeding: no ongoing restoration effort in red circles, strong ongoing seeding in green triangles ($\mu_S = 0.7$), and weak ongoing seeding in blue squares ($\mu_S = 0.1$). Panel a) shows the change in spread rate as the initial kelp density varies, and panel b) shows the change in spread rate as the initial urchin density varies.

kelp oasis (L) through kelp outplanting enhances kelp recovery rate, the spatial scale of ongoing restoration efforts (η) has a minimal impact over kelp recovery rate.

4.4. Discussion

In our model of kelp restoration, scaling up ecologically on restoration efforts can have a bigger effect in restoration success than scaling up spatially or temporally. One of the key factors in determining if kelp recovery will be possible is the threshold urchin density, which our model suggests is mostly determined by local interactions. Because we incorporated kelp-urchin grazing

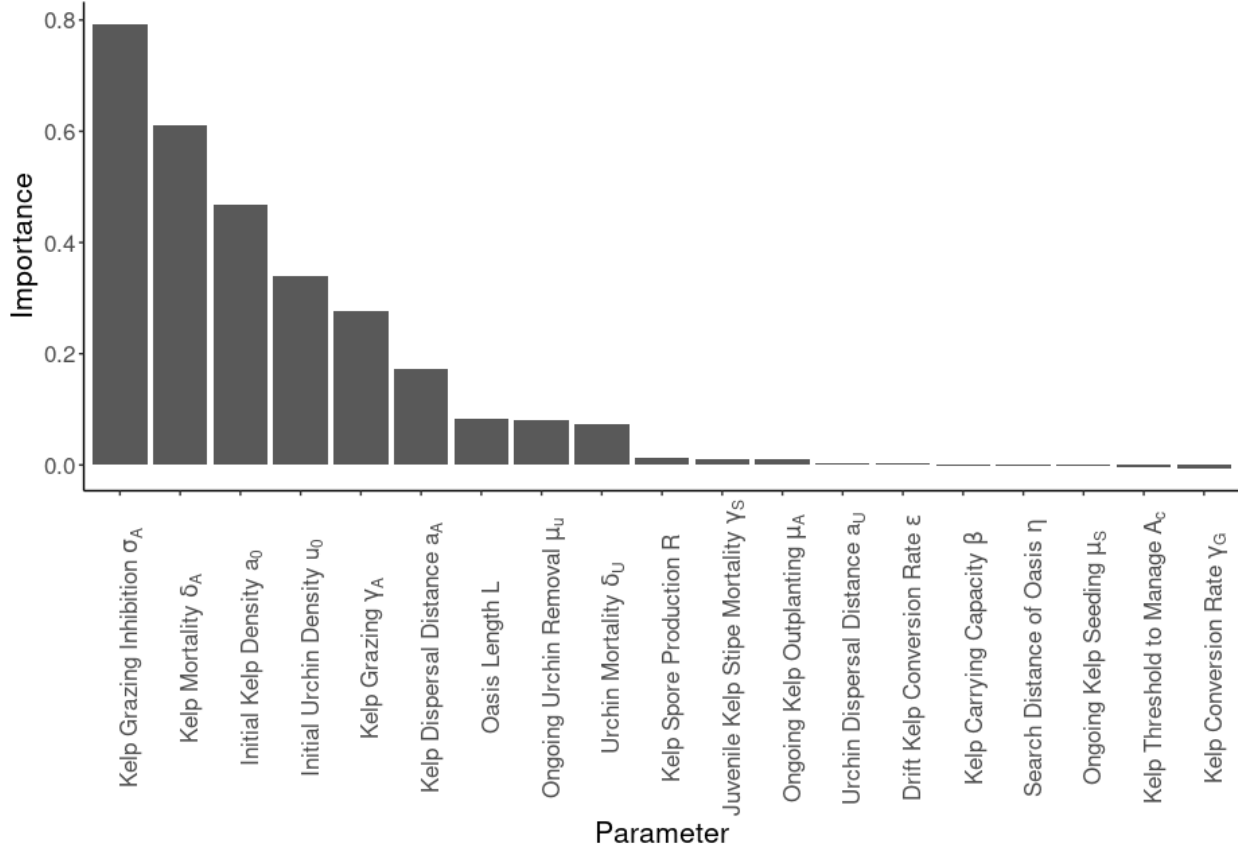


FIGURE 4.8. Importance ranking of the parameters of the Model 4.1 from the global sensitivity analysis of the kelp recovery rate. See Table 4.1 for more detailed parameter definitions.

feedbacks that can drive alternative stable states, kelp recovery does not occur in our model unless urchin density is below a certain value (Figure 4.3). This threshold increases as kelp density increases, i.e. kelp outplanting reduces the amount of urchin removal necessary for recovery. In addition, improving the initial conditions through an increase in kelp density or decrease in urchin density at an early stage can enhance kelp recovery rate more than ongoing restoration efforts (compare Figures 4.5 and 4.7). This suggests that a Field of Dreams approach can apply in kelp forest restoration, as in our model enhancing the ecological conditions at a short temporal scale and small spatial scale has more impact than distributing restoration efforts through a longer period of time or to a greater spatial extent.

The theoretical results of the different restoration outcomes are consistent with what has been observed in kelp restoration efforts. In recent restoration efforts in our focal system of Northern California, sites where urchin removal has been implemented below a threshold density of 2 urchins/m² had seen significantly higher kelp density compared to sites without urchin removal [139]. While these restoration sites and regions of improved recovery cover a much smaller spatial scale compared to original loss (compare [118] to [139]) due to resource limitation, they can facilitate kelp recovery in targeted locations of economic importance (e.g. near ports) to coastal stakeholders such as the fishing and diving communities. In Southern California, sea urchin removal can increase the success of kelp reseeding [43]. Beyond California, [81] found that urchin removal and kelp outplanting had been successful restoration methods for increasing kelp density in different regions of the Australian coastline. In the case of kelp reintroduction on the coast of Tasmania, [121] found greater success of kelp outplants in areas with urchin removal.

This predominant role of early restoration efforts also parallels empirical findings in systems beyond the kelp system modeled here. For example, in [82] restoring the habitat of anurans (wetlands) at a small spatial and temporal scale was enough to allow eventual recovery of community composition and diversity of amphibians. In [18], thinning of the forest at an early stage led to an increase in the density of certain bird populations compared to unthinned (Figure 4.7). These cases where a Field of Dreams approach is successful have in common that the habitat quality is one of the main limiting factors of restoration success. In the case of kelp forest restoration, a suitable habitat is determined by the active grazer density (purple urchins in our study system).

The predominance of early restoration efforts, and greater efficacy of ecological scaling up over spatial or temporal scaling up in restoration efforts, arises, in part, because of the threshold dynamics in our model with alternative stable states. As described above, with these threshold dynamics, once initial restoration passes the threshold, which depends on both urchin and kelp densities, then natural recovery can occur. The potential for alternative stable states arises from our Type IV (unimodal) functional response in urchin grazing to kelp density, which might occur due to an urchin grazing behavioral shift from active to passive grazing due to greater subsistence on drift kelp or cryptic behavior with higher densities of kelp and associated urchin predators [70]. Accordingly, our global sensitivity analyses indicates that the parameters that shape urchin grazing

response to kelp density comprise the main driving factors of both the possibility of recovery and its rate. If, in reality, this feedback between kelp density and urchin density is not strong enough to drive alternative stable states, we would expect a reduction in the overall role of active grazing behavior and a potential increase in the role of greater spatial and temporal scales of restoration efforts. That said, our best-fit model did find a strong enough feedback between kelp density and urchin grazing for alternative stable states to occur, and [97] provide empirical support of a significant role of urchin grazing in kelp decline on the California north coast, where including urchin grazing into a partial least squares regression analysis doubled the variability in the yearly data of kelp coverage explained by the model. In addition, as noted above, data from restoration efforts indicate that urchin removal can increase restoration success in an number of kelp systems spanning California and Australia [43, 81, 121, 139]. Further evidence for a role for urchin densities in kelp dynamics include rapid kelp recovery following urchin mass mortality in southern California [144] and rapid kelp declines following urchin range expansions in Tasmania [86]. In Tasmania, both theory and data suggest that alternative stable states between urchin barrens and kelp forests affect recovery success, analogous to our model [66, 86, 92].

Although increasing the temporal scale of restoration has a smaller effect on the ability of kelp to recover in our deterministic simulations, an increase in the temporal scale of restoration can buffer against the potential for short-term restoration failure from caused by extreme, stochastic events [112]. In the case of kelp, an increase in the likelihood of marine heatwaves can lead to potential die-offs of kelp and increases in urchin recruitment, which might bring urchin density above the threshold and restrict kelp recovery [118]. This potential for restoration failure due to environmental stochasticity has been noted in amphibian [33] and plant [31] reintroductions, and has been observed in coral reef restoration failing due to hurricane activity [14].

Finally, partial restoration efforts leading to longer-term, larger scale recovery will depend on the spatial extent of the dispersal and the temporal scale of generation time of the ecological components. For example, long river systems may require a timeframe in the scale of decades to reestablish their hydrological dynamics [129]. In addition, active interventions may reduce the impact of ecological traps produced by restoration efforts [52]. For example, [124] found the butterfly *Lycaena xanthoides* to selectively oviposit more frequently and with more eggs in

seasonally-flooded habitats with lower egg survival, as compared to adjacent non-flooded habitats where a tall invasive grass obscured native plants. Averting this accidental cue to poor ovipositing habitat would likely require scaling up of restoration to also incorporate invasive species removal in non-flooded habitats. More generally, active management approaches to account for ecological traps may include changing the behavior of the animals by removing cues or habituating the animals to ignore the cues provided by ecological traps [52].

4.4.1. Management implications. In our model, the most effective restoration approach for kelp forest in northern California is a combination of reduction of purple urchin density through urchin removal and increase of bull kelp density through adult kelp outplanting at an early stage of the restoration project. The role of any ongoing restoration efforts, including further urchin removal and kelp outplanting, as well as kelp seeding was highly sensitive to initial kelp density (Figures 4.5 and 4.6), which supports targeting such efforts around extant kelp “oases”. In the absence of any oases, kelp recovery might further rely on initial kelp reseeding or outplanting restoration interventions, depending on the potential for a spore bank as discussed in the “Model limitations” section below. Ongoing restoration efforts might play a greater role if initial removals are insufficient to pass the threshold for kelp recovery or, as noted above, future extreme climate events might disrupt restored populations.

Urchin removal is a technique that is already being applied in the northern coast of California [61]. Our results suggest that these efforts are more likely to be successful when complemented with kelp outplanting. Transplantation of *N. luetkeana* has been successfully applied further north in the coast of Washington, where transplanting of juveniles of natural populations was more successful than cultured kelp [21]. The effectiveness of outplanting cultured kelp or juveniles of natural populations is still an open question in the highly exposed Sonoma and Mendocino County coastlines [47].

In other rocky reef systems, kelp forest restoration success has been determined by kelp introduction and removal of stressors (such as active grazers) [100]. Kelp introduction was a determinant for the success of *Lessonia nigrescens* restoration in the northern coast of Chile [25]. Previous work has shown that younger kelp sporophytes are more prone to predation [90]. Thus, identifying how

to minimize urchin predation on younger transplants or outplants is key to ensuring successful introduction of kelp. Previous studies have proposed using grazer exclusion devices [21] or choosing sites where grazers are not as highly abundant can benefit kelp introduction [34]. The sensitivity of our model to urchin grazing rate further supports the potential efficacy of such approaches.

While our model can provide qualitative management-relevant insights into the relative efficacy of different approaches (e.g. initial vs. ongoing interventions; urchin removal, kelp reseeding, and kelp outplanting separately or in combination), quantitatively precise insights, such as the exact urchin threshold and kelp densities that can enable recovery, are more challenging due to data limitations. Our best-fit model has wide-ranging posterior distributions for most parameters (Figure B.1), including those that strongly influence the threshold urchin and kelp densities for recovery such as the urchin grazing rate on kelp. In addition, these parameters will inevitably vary in space and time, such as through urchin grazing dependence on water temperature and sedimentation [130], such that no one target value will apply. Our sensitivity analysis can inform data collection aimed at resolving parameters (and their environmental dependencies) most likely to improve the ability to precisely estimate target values for urchin removal and kelp reintroduction. As more data becomes available from both kelp recovery monitoring and monitoring of potential abiotic drivers at finer spatial and temporal scales, our model (with extensions to address the assumptions described in the “Model limitations” section below) provides a foundational quantitative framework for leveraging those data for more precise predictions of threshold values for achieving a target recovery likelihood or rate.

Another consideration for kelp restoration management, especially in northern California, is the reintroduction of predators such as the sunflower seastar. A role for predator reintroduction is evident in the high sensitivity of the recovery threshold and rate in our model to parameters that likely depend on predator presence: urchin mortality (δ_A) and the potential for urchins to switch between active and passive grazing (σ_A). If the urchin grazing mode depends on a cryptic behavioral response to predator presence [26, 35] as well as drift kelp presence [55], then predator reintroduction could increase system resilience in terms of both likelihood and rate of recovery. Empirically, predator decline was one of the identified drivers of kelp forest loss in northern California [97, 118],

such that predator reintroduction is then a component of addressing the drivers of system degradation, which is a key determinant of restoration success [100, 108]. As noted in the Methods: Model overview, we did not explicitly include predator reintroduction because of uncertainty in its near-term feasibility and because initial restoration to a kelp-dominated system with non-barren, nutritious urchins through the interventions modeled here might determine predator reintroduction success. Therefore, while our model can provide insight into restoration management on the short (annual) time scales modelled here, understanding the potential long-term recovery of ecosystem structure and resilience will likely require consideration of predator dynamics and reintroduction.

Our findings provide a system-specific case study of threshold-based approaches illuminated in previous theoretical models that look at the optimal restoration strategy of partial restoration efforts. [77] suggest that an economically optimal approach is to engage in restoration efforts until the target population reaches a certain threshold (the urchin threshold density in our case). In our work we find two key restoration strategies to perform at early stages of restoration: urchin removal and kelp outplanting. [78] further suggest that the optimal restoration strategy is to implement one strategy until a certain threshold is reached (removing urchins below the urchin threshold density), and then combining the two strategies until a certain “investment benchmark” is achieved, after which the system (e.g. kelp forest) will recover from natural processes. This benchmark might be determined in terms of a minimum kelp density or a maximum urchin density in the restored kelp oasis. Budget limitations may restrict the number of target sites that can be successfully restored [145], which makes choosing priority sites based on likelihood of restoration success an important step when performing restoration. Finally, the three strategies explored in this work might have an optimal timing of when to be applied, which likely differs for each strategy [79]. Finding the optimal timing of application of the three strategies explored in this work and other unexplored strategies is still an open question.

4.4.2. Model limitations. As with any model, we made a number of assumptions to construct the simplest possible model relevant to our central questions. We have chosen a Laplacian dispersal kernel, but dispersal of kelp seeds is known to be highly dependent on currents, which may skew the direction of dispersal [46]. With advection, kelp spread rate would likely increase in favor of the direction of the current [89], dependent on physical factors such as seed buoyancy and water

turbulence. These physical factors could be further explored using a non-parametric kernel [115]. We also ignore adult urchin movement, where the effect will depend on urchin movement responses to kelp recovery, where urchins exhibit lower movement inside than outside kelp forests due to differences in food availability [93]. If kelp recovery reduces urchin movement due to increased drift kelp availability, then accounting for urchin movement might decrease the amount of urchin removal and the role of ongoing restoration in restoration efficacy. Alternatively, if recovering kelp attracts high-movement barren urchins as active grazers, then accounting for urchin movement might increase the amount of urchin removal and the role of ongoing restoration in restoration efficacy.

Other physical factors that are not considered explicitly in this model are variations in environmental conditions such as temperature and nutrients, which are known to affect kelp productivity and growth [11]. Our sensitivity analyses show that parameters highly dependent on environmental conditions in our model such as kelp mortality (δ_A) are influential in determining both the urchin density threshold and kelp recovery rate. Thus, both urchin threshold density and kelp recovery rate might be higher at regions of the coastline with environmental conditions that further enhance kelp survival, leading to location-specific restoration intervention intensity required for success. If stable in time, local variation in environmental conditions could also help identify regions of the coastline with a higher potential to become kelp oases [60].

Our model also assumes that the effects of ongoing restoration effort occur instantaneously. In reality, restoration efforts might present lags in their impact for reasons such as long life-cycles of the target population [133] or natural lags in the biogeochemical cycles [53]. For kelp, a lag between seed outplanting and sporophyte establishment and maturation, during when kelp outplants might be more vulnerable to urchin grazing [4], captured in our model with a separate grazing rate γ_S , could decrease the efficacy of seed outplanting modelled here.

In addition, we focus our model on the dynamics of kelp sporophytes and implicitly considers the dynamics of the gametophytes. Gametophytes have the potential to act as a spore bank similar to a terrestrial seed bank, with persistence in a dormant state for an extended period of time until favorable environmental conditions occur [39]. This could enable kelp recovery in the absence of the extant “kelp oases” modeled here and lead to the alternative stable states observed in our model to

behave as long transients instead [8]. In this case, management might focus on how to decrease the length of the urchin barren transient state while also increasing the length of the kelp forest transient state, if a goal is to avoid extended periods of economic loss from kelp-associated livelihoods such as the red urchin commercial fishery, red abalone recreational fishery, and recreational diving. While analyzing the effect of different restoration interventions on transient duration given a kelp spore bank would require model modifications, given the importance of the grazing interaction between kelp and urchins found here, we suspect the qualitative results of our model would not change significantly.

Our best-fit model also assumes that alternative stable states are relevant to the kelp-urchin dynamics observed in our system. Preliminary evidence suggests kelp is returning to some areas of the coastline, potentially due to more nutrient-rich, colder waters (Brent Hughes, personal communication). This recovery could be due to a shift in environmental conditions from a range where alternative stable states were relevant to a range where the kelp-dominated is the only relevant state. Alternatively, this recovery might indicate that the system state shifts with environmental conditions without alternative stable states. While these alternative explanations affect the relevance of our results concerning a threshold value of urchin density or kelp reintroduction that enables recovery, in either case restoration might still affect the rate of recovery, as observed in northern California [139], especially if transients are slow as noted above. Determining which case best explains this apparent recovery will require analyzing the emerging data in the coming years in comparison to model predictions with environmental drivers and different model structures with or without alternative stable states (as done for giant kelp in southern California in [70], where there is greater data availability than for the northern California bull kelp system that is our focus here).

Our model considers only the interactions between sea urchins and kelp, which are central to the efficacy of current restoration interventions. In reality, an array of other species in California's temperate rocky reefs might affect recovery dynamics and restoration outcomes. For example, crustose coralline algae competing with kelp may also facilitate urchin recruitment, potentially decreasing the threshold urchin density, i.e. increase the urchin removal necessary for kelp recovery [9]. In comparison, the presence of a natural predator of sea urchins such as the sunflower sea star

(currently functionally extinct on the California north coast [118]) would lead to a more cryptic behavior of urchins, which would lead to an increase in threshold urchin density [125]. Adding such predators and their potential reintroduction can add another ecological dimension to restoration, as discussed above in the section on Model implications. Therefore, further adding ecological realism can allow extensions in the capacity of our model to inform restoration efforts.

Parameter	Description	Range of Possible Values Explored	Best-fit Value
δ_A	Survival probability of adult kelp	[0, 1]	0.510
γ_A	Grazing intensity of urchins on kelp	[0, 1]	0.101 kelp m ⁻² urchins ⁻¹
σ_A	Inversely determines kelp density at maximum urchin grazing	[0, 100]	15.475 kelp m ⁻²
γ_S	Probability of juvenile kelp stipes being grazed by urchin	[0, 100]	0.743 urchins ⁻¹
β	Inverse of maximum kelp density	Estimated without ABC (see text)	2.42 kelp m ⁻²
a_A	Inverse of mean dispersal distance of kelp	[0, 100]	16.137 m ⁻¹
R	Per capita spores production of kelp	[0, 10]	5.500
δ_U	Survival probability of urchins	[0, 1]	0.312
γ_G	Urchin production from direct kelp consumption	[0, 10]	4.956 urchins
a_U	Inverse of mean dispersal distance of urchin	[0, 100]	93.586 m ⁻¹
ε	Urchin production from kelp consumed by urchins as drift kelp	[0, 10]	9.484 kelp m ⁻²
μ_U	Intensity of urchin removal relative to natural urchin mortality	[0, 1]	
μ_S	Intensity of kelp seeding relative to per capita spores production	[0, 1]	
μ_A	Intensity of kelp outplanting relative to natural kelp mortality	[0, 1]	
η	Length of region to apply restoration efforts around a kelp oasis	[0, 100]	
A_c	Critical kelp density to identify where to apply restoration efforts	[0, 1]	
A_0	Initial kelp density at the kelp oasis	[0, 5]	
U_0	Initial urchin density at the coastline	[0, 100]	

TABLE 4.1. Description of each of the parameters of the model.

APPENDIX A

Fixed points of System 3.5 and their stability

The fixed points of System 3.5 (p, n) satisfy the equations

$$\begin{aligned} p &= \delta_p p + \gamma_p \frac{pn}{1 + \sigma n^2} \\ n &= \delta_n n \exp\left(-\frac{\gamma_n p}{1 + \sigma n^2}\right) + Rn \frac{\exp(-p)}{1 + n}. \end{aligned}$$

If $p = 0$, then the second equation gives us two solutions for n , $n = 0$ and

$$(A.1) \quad n^* = \frac{R}{1 - \delta_n} - 1.$$

If $p \neq 0$, then the first equation has two solutions for n given by

$$(A.2) \quad n^{\vee\wedge} = \frac{\gamma_p}{2(1 - \delta_p)\sigma} \left(1 \pm \sqrt{1 - \frac{4\sigma(1 - \delta_p)^2}{\gamma_p^2}} \right)$$

where n^\vee corresponds to the solution with a $-$ sign and n^\wedge to the solution with a $+$ sign. These solutions are positive whenever $\gamma_p \geq 2\sqrt{\sigma}(1 - \delta_p)$. In such case, plugging $n^{\vee\wedge}$ into the second equation provides us with the following expression:

$$\delta_n \exp\left(-\frac{\gamma_n p}{1 + \sigma n^{\pm 2}}\right) + \frac{R}{1 + n^{\vee\wedge}} \exp(-p) = 1.$$

Then there is an unique value $p^{\vee\wedge}$ that solves the trascendental equation

$$(A.3) \quad p^{\vee\wedge} = \log\left(\frac{R}{(1 + n^{\vee\wedge}) \left(1 - \delta_n \exp\left(-\frac{\gamma_n p^{\vee\wedge}}{1 + \sigma n^{\pm 2}}\right)\right)}\right).$$

This equation in p has an unique solution as the function

$$(A.4) \quad f(p) = p - \log \left(\frac{R}{(1 + n^{\vee\wedge}) \left(1 - \delta_n \exp \left(-\frac{\gamma_n p}{1 + \sigma n^{\pm 2}} \right) \right)} \right)$$

is monotonic for p and satisfies $\lim_{p \rightarrow -\infty} f(p) < 0$ and $\lim_{p \rightarrow \infty} f(p) > 0$. For it to be biologically relevant, we also require $\lim_{p \rightarrow 0} f(p) < 0$, which will occur when

$$(A.5) \quad R > (1 - \delta_n)(1 + n^{\vee\wedge})$$

or, after reorganizing the terms, $n^{\vee\wedge} < n^*$.

The Jacobian of the system J is the following:

$$(A.6) \quad J(p, n) = \begin{pmatrix} \delta_p + \gamma_p \frac{n}{1 + \sigma n^2} & \gamma_p p \frac{1 - \sigma n^2}{(1 + \sigma n^2)^2} \\ -\frac{\delta_n \gamma_n n}{1 + \sigma n^2} \exp \left(-\frac{\gamma_n p}{1 + \sigma n^2} \right) - \frac{R n \exp(-p)}{1 + n} & \delta_n \exp \left(-\frac{\gamma_n p}{1 + \sigma n^2} \right) \left(1 + \frac{2\sigma \gamma_n p n^2}{(1 + \sigma n^2)^2} \right) + \frac{R \exp(-p)}{(1 + n)^2} \end{pmatrix}.$$

From here, the extinction equilibrium satisfies

$$(A.7) \quad J(0, 0) = \begin{pmatrix} \delta_p & 0 \\ 0 & \delta_n + R \end{pmatrix}$$

which has eigenvalues $\delta_p < 1$ and $\delta_n + R > 1$. Therefore the extinction equilibrium is a saddle. For the resource-only equilibrium, the upper right term of the Jacobian matrix equals 0 whenever $p = 0$. Therefore $J(0, n^*)$ is a triangular matrix, with the eigenvalues being the diagonal terms

$$(A.8) \quad \lambda_1 = \delta_p + \gamma_p \frac{n^*}{1 + \sigma n^{*2}},$$

$$(A.9) \quad \lambda_2 = \delta_n + \frac{(1 - \delta_n)^2}{R}.$$

Because $R > 1 - \delta_n$, $0 < \lambda_2 < 1$. λ_1 , on the other hand, λ_1 will produce a change in stability when

$$(A.10) \quad \gamma_p = \gamma_p^* = (1 - \delta_p) \frac{1 + \sigma n^{*2}}{n^*}.$$

In this case, the equilibrium is stable whenever $\gamma_p < \gamma_p^*$ and a saddle when $\gamma_p > \gamma_p^*$. Because $n^* > 1/\sqrt{2\sigma}$, plugging $\gamma_p = \gamma_p^*$ in Equation A.2, we have that $n^* = n^\wedge$. Based on the conditions for (p^\wedge, n^\wedge) to be biologically reasonable, this implies that at $\gamma_p = \gamma_p^*$, the system goes through a transcritical bifurcation, where the carrying capacity $(0, n^*)$ changes stability.

The transcendental equation that describes $p^{\vee\wedge}$ renders it impossible to analyze them directly. However, a numerical exploration in Figure A.6 shows that these equilibria are unstable for $\gamma_p < \gamma_p^*$ and (p^\wedge, n^\wedge) becomes stable for $\gamma_p > \gamma_p^*$. Combining this result with the condition for the equilibrium point (p^\wedge, n^\wedge) to be biologically relevant (Equation A.5), we find that when $\gamma_p > \gamma_p^*$, there are no fixed points in the first quadrant (i.e. \mathbb{R}_+^2).

This transcritical bifurcation occurs with almost any combination of parameters in our region of interest. To show this, we perform a similar analysis as those in [74, 102]. When $\gamma_p = \gamma_p^*$, we can rewrite our system in diagonal form and centered around the origin by making the change of variables:

$$(A.11) \quad x_m = \frac{\lambda_2 - 1}{n^* \left(1 - \delta_n + \frac{\delta_n \gamma_n}{1 + \sigma n^{*2}}\right)} p_m$$

$$(A.12) \quad y_m = p_m + n_m - n^*$$

provided that $\left(1 - \delta_n + \frac{\delta_n \gamma_n}{1 + \sigma n^{*2}}\right) \neq 0$. Otherwise, we let $x_m = p_m, y_m = n_m - n^*$. In both cases, this lets us write our System 3.5 as

$$(A.13) \quad \begin{pmatrix} x_{m+1} \\ y_{m+1} \end{pmatrix} = \begin{pmatrix} 1 & 0 \\ 0 & \lambda_2 \end{pmatrix} \begin{pmatrix} x_m \\ y_m \end{pmatrix} + \text{h.o.t.}$$

We can expand this system to include the parameter as a dynamical factor with eigenvalue 1 as $\mu_m \equiv \gamma_p - \gamma_p^*$. The central limit theorem gives us that $y_m = h(x_m, \mu_m)$ for some function $h = O((x_m + \mu_m)^2)$. Because x_m is a multiple of p_m , its dynamics follow the same trend, and can be approximated up to $O((x_m + \mu_m)^3)$ as:

$$(A.14) \quad x_{m+1} = f(x_m, \mu_m) = x_m + \frac{\gamma_p^*(1 - \sigma n^{*2})}{(1 + \sigma n^{*2})^2} x_m^2 + \frac{\sigma n^{*2}(n^* - \gamma_p^*)}{(1 + n^{*2})^2} x \mu_m + O((x_m + \mu_m)^3)$$

Equation A.14 satisfies that $f_x(0, 0) = 1, f_\mu(0, 0) = 0, f_{xx}(0, 0) \neq 0$ Because we assume that $n^* > 1/\sqrt{\sigma}$, and $f_{x\mu}(0, 0) \neq 0$ except when $n^* = \gamma_p^*$. Plugging this value Equation 3.6, we get that the condition $n^* = \gamma_p^*$ holds only when $n^* = \sqrt{\frac{1-\delta_p}{\sigma\delta_p}}$.

Therefore, whenever $n^* \neq \sqrt{\frac{1-\delta_p}{\sigma\delta_p}}$, the system goes through a transcritical bifurcation between $(0, n^*)$ and (p^\wedge, n^\wedge) as γ_p passes through γ_p^* .

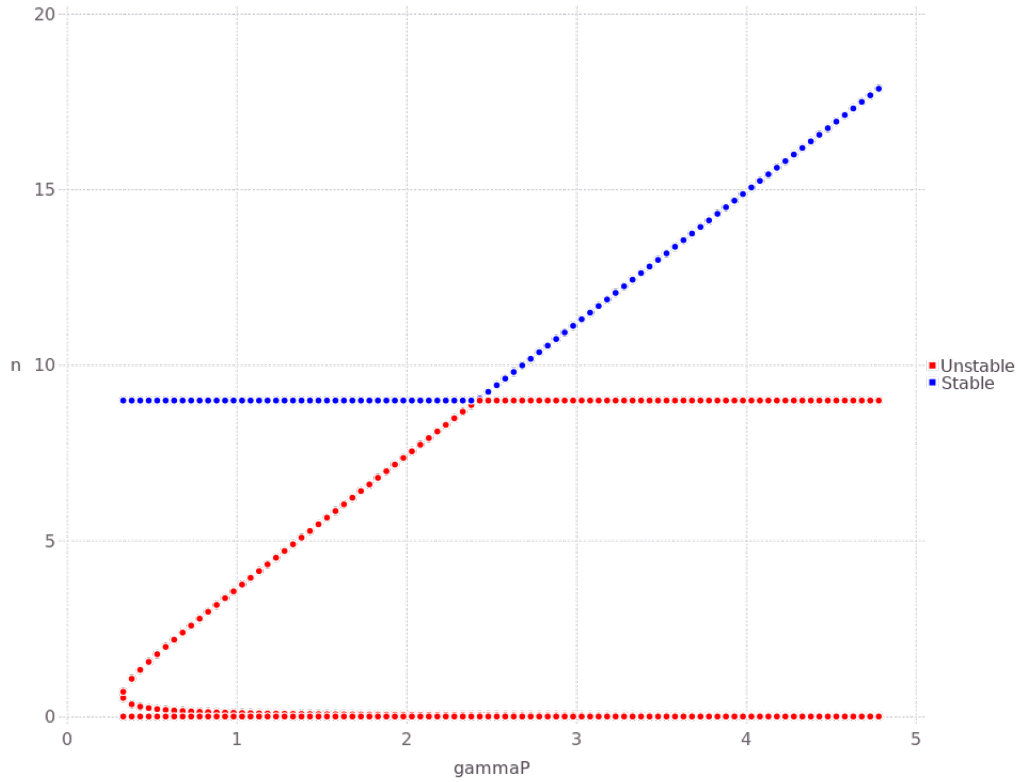


FIGURE A.1. Numerical values of different equilibria for n and their stability as we vary γ_p in our region of interest. The red points correspond to unstable equilibria, whereas the blue points correspond to stable equilibria. In this figure, $\delta_p = 0.9$, $\sigma = 2.67$, $\delta_n = 0.8$, $\gamma_n = 1$, $R = 2$.

APPENDIX B

Proof of Theorem 3.3.1

If $p_0 = O(\varepsilon^{-1})$, plugging $O(\varepsilon^{-1})$ into the formula for n_1 gives us that $n_1 = o(\varepsilon)$. Plugging $o(\varepsilon)$ into the formula for p_2 gives us that:

$$(B.1) \quad p_2 = \delta_p p_1 + o(\varepsilon).$$

In addition, if $n_m = o(\varepsilon)$, the equation for n_{m+1} satisfies:

$$(B.2) \quad \frac{n_{m+1}}{n_m} = O(\delta_n \exp(-\gamma_n p_m) + R \exp(-p_m)).$$

While $p_m = O(\varepsilon^{-1})$, this expression will satisfy $n_{m+1}/n_m < 1$. We can thus assume that the expression

$$(B.3) \quad p_{m+1} = \delta_p p_m + o(\varepsilon)$$

is satisfied until $p_{m+1} = O(1)$. Therefore, when $p_m = O(\varepsilon^{-1})$, the consumer population time evolution can be approximately solved as

$$(B.4) \quad p_m = \frac{\delta_p^m}{\varepsilon} + o(\varepsilon).$$

This expression stops working when $p_m = O(1)$, and thus resource will start a recovery afterwards. We can estimate the order of magnitude of such m by plugging $p_m = 1$ above. Solving for m gives us that

$$(B.5) \quad m = \frac{\log(\varepsilon)}{\log(\delta_p)}$$

which is the expression that proves the theorem.

APPENDIX C

Proof of Theorem 3.3.2

To show the existence of this theorem, we use Theorem 2.9 of [91]. To do this, we consider the first quadrant M as a metric subspace of \mathbb{R}^2 with metric $d(x, y) = \|x - y\|_2$ induced by the Euclidean norm. Let $T : M \rightarrow M$ be given by

$$(C.1) \quad T \begin{pmatrix} p \\ n \end{pmatrix} = \begin{pmatrix} p \left(\delta_p + \frac{\gamma_p n}{1 + \sigma n^2} \right) \\ n \left(\delta_n \exp \left(-\frac{\gamma_n p}{1 + \sigma n^2} \right) + \frac{R \exp(-p)}{1 + n} \right) \end{pmatrix}.$$

We show that T is a point dissipative, compact map on M . Because M is a subspace of \mathbb{R}^2 , compactness is trivial. A map is point dissipative if there is a bounded set $B_0 \subset M$ such that B_0 attracts each point in M . To show T is point dissipative, we find such bounded set B_0 .

Let

$$(C.2) \quad \begin{aligned} f_p(n) &= \delta_p + \frac{\gamma_p n}{1 + \sigma n^2}, \\ f_n(p, n) &= \delta_n \exp \left(-\frac{\gamma_n p}{1 + \sigma n^2} \right) + \frac{R \exp(-p)}{1 + n}. \end{aligned}$$

Note that $f_n < 1$ whenever $n > n^*$, where n^* is given by Equation A.1. This implies that n is attracted by the set $[0, n^*]$. Without loss of generality, we assume that $n \in [0, n^*]$. Suppose that $p > p^*$, where p^* is

$$(C.3) \quad p^* = \max \left(\frac{1 + \sigma n^{*2}}{\gamma_n}, 1 \right) = \frac{1}{\varepsilon}.$$

A similar argument to that of the proof for Theorem 3.3.1 shows that in this case, the consumer population will satisfy $p = O(1)$ in time $\ln(\varepsilon)/\ln(\delta_p)$. In particular, $p < p^*$ after a period of time. In addition, if $p < p^*$ but $Tp > p^*$, f_p satisfies:

$$(C.4) \quad f_p(n) \leq \delta_p + \frac{\gamma_p}{2\sqrt{\sigma}}$$

for any n . This implies that $Tp \leq \left(\delta_p + \frac{\gamma_p}{2\sqrt{\sigma}}\right)p^*$. Let τ be the period of time such that $T^\tau \left(\delta_p + \frac{\gamma_p}{2\sqrt{\sigma}}\right)p^* < p^*$. Therefore p is attracted by the set $[0, (\delta_p + \frac{\gamma_p}{2\sqrt{\sigma}})^\tau p^*]$. Then, the bounded rectangle

$$(C.5) \quad B_0 := \left[0, \left(\delta_p + \frac{\gamma_p}{2\sqrt{\sigma}}\right)^\tau p^*\right] \times [0, n^*]$$

is an attracting set in M . Therefore, T is a point dissipative map.

Therefore, Theorem 2.9 of [91] implies that there is a compact global attractor in M . Finally, Because M is locally connected, Theorem 4.5 of [48] implies that the global attractor is connected, which completes the proof.

APPENDIX D

Proof of Theorem 3.3.3

Let $x_m = p_m, y_m = n^* - n_m$. Because $\|(x_m, y_m)\| = O(\varepsilon)$, System 3.5 can be approximated by the linearized system:

$$(D.1) \quad \begin{pmatrix} x_{m+1} \\ y_{m+1} \end{pmatrix} \sim J(0, n^*) \begin{pmatrix} x_m \\ y_m \end{pmatrix},$$

where the Jacobian $J(0, n^*)$ is described by Equation A.6. The calculations of Appendix A show that the Jacobian $J(0, n^*)$ is a lower triangular matrix, with eigenvalues

$$(D.2) \quad \lambda_1 = \delta_p + \gamma \frac{n^*}{1 + \sigma n^{*2}}.$$

$$(D.3) \quad \lambda_2 = \delta_n + \frac{(1 - \delta_n)^2}{R}$$

and eigenvectors

$$(D.4) \quad v_1 = \begin{pmatrix} u \\ 1 \end{pmatrix}, v_2 = \begin{pmatrix} 0 \\ 1 \end{pmatrix}$$

where

$$(D.5) \quad u = \frac{\lambda_2 - \lambda_1}{n^* \left(1 - \delta_n + \frac{\delta_n \gamma n^*}{1 + \sigma n^{*2}} \right)}.$$

This system has for solution the expression

$$(D.6) \quad \begin{pmatrix} x_m \\ y_m \end{pmatrix} = a\lambda_1^m v_1 + b\lambda_2^m v_2,$$

where a, b are constants. If we let $m = 0$, then we can solve the linear system

$$(D.7) \quad \begin{pmatrix} \varepsilon \\ \varepsilon \end{pmatrix} = \begin{pmatrix} u & 0 \\ 1 & 1 \end{pmatrix} \begin{pmatrix} a \\ b \end{pmatrix},$$

which has solutions

$$(D.8) \quad \begin{pmatrix} a \\ b \end{pmatrix} = \begin{pmatrix} \frac{1}{u} & 0 \\ -\frac{1}{u} & 1 \end{pmatrix} \begin{pmatrix} \varepsilon \\ \varepsilon \end{pmatrix}.$$

In particular, this gives us that $a = \frac{\varepsilon}{u}$. Because $\gamma_p > \gamma_p^*$, then $\lambda_1 > 1$, and $\lambda_2 < 1$. Therefore, for big m , System D.6 can be approximated as

$$(D.9) \quad \begin{pmatrix} x_m \\ y_m \end{pmatrix} \sim a\lambda_1^m v_1 = \frac{\varepsilon\lambda_1^m}{u} \begin{pmatrix} u \\ 1 \end{pmatrix}.$$

Thus, System 3.5 will stay near the resource-only equilibrium as long as $\|(x_m, y_m)\| = O(\varepsilon)$. In particular, the System will escape the saddle point when $x_m = O(1)$. Plugging in $x_m = 1$ into the approximated solution lets us find M that solves the equation

$$(D.10) \quad 1 = \varepsilon\lambda_1^M.$$

This has for solution

$$(D.11) \quad M = \frac{\log\left(\frac{1}{\varepsilon}\right)}{\log(\lambda_1)}$$

which is the expression that proves the theorem.

APPENDIX E

Presence of alternate stable states in the nonspatial version of Model 4.1

In this appendix we show the presence of alternate stable states in our model by showing it has trajectories at where kelp recovers (kelp forest state) and where kelp collapses (urchin barren) at different initial conditions. To show these trajectories, we run our spatial model 4.1 and then calculate the total kelp density (denoted by \mathbf{A}_t) and urchin density (denoted by \mathbf{U}_t) by integrating their densities at each point y over the entire coastline. In mathematical terms, we calculate these total densities using the expressions:

$$(E.1) \quad \mathbf{A}_t = \int_{\Omega} A_t(y) dy,$$

$$(E.2) \quad \mathbf{U}_t = \int_{\Omega} U_t(y) dy.$$

Figure E.1 provides trajectories of total kelp and urchin densities after 24 time steps under a range of values for initial kelp and urchin densities (and with the same set of parameter values for all simulations). These simulations demonstrate the existence of two alternative steady-state outcomes in the model: the time series converge to either (a) a limit cycle of high kelp density and urchin persistence (kelp forest state) or (b) a barren state where kelp declines to regional extinction and the urchins initially increase but eventually collapse due to starvation. Which of these states is the long-term outcome depends on initial kelp and urchin densities relative to the threshold values identified in Fig. 3.

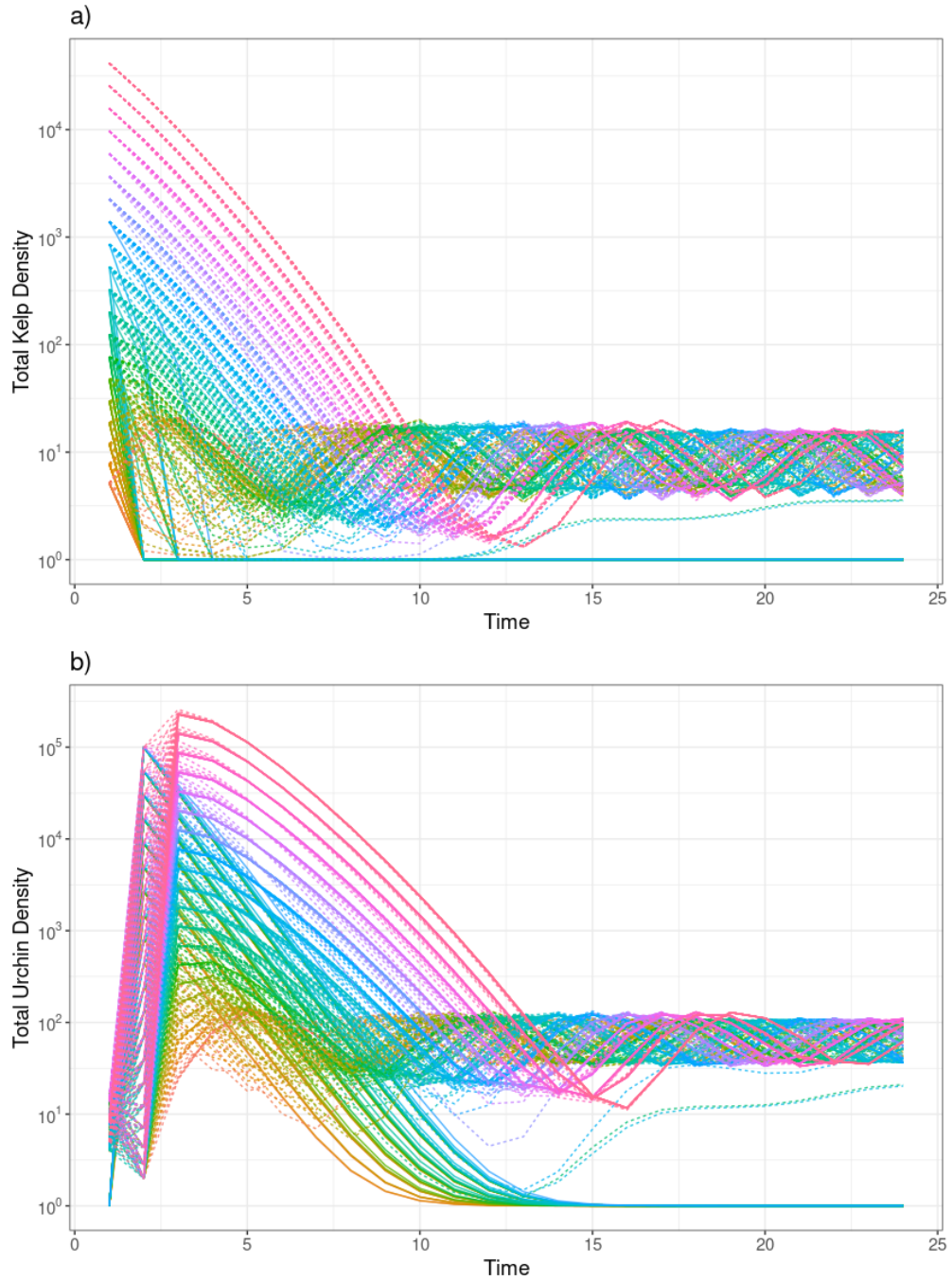


FIGURE E.1. Trajectories of **a)** total kelp (\mathbf{A}_t) and **b)** urchin (\mathbf{U}_t) densities. Each color represents different initial conditions, the solid lines represent trajectories that converge into an urchin barren, while the dashed lines represent trajectories that converge into a kelp forest state.

APPENDIX F

Posterior distributions of parameters of Model 4.1

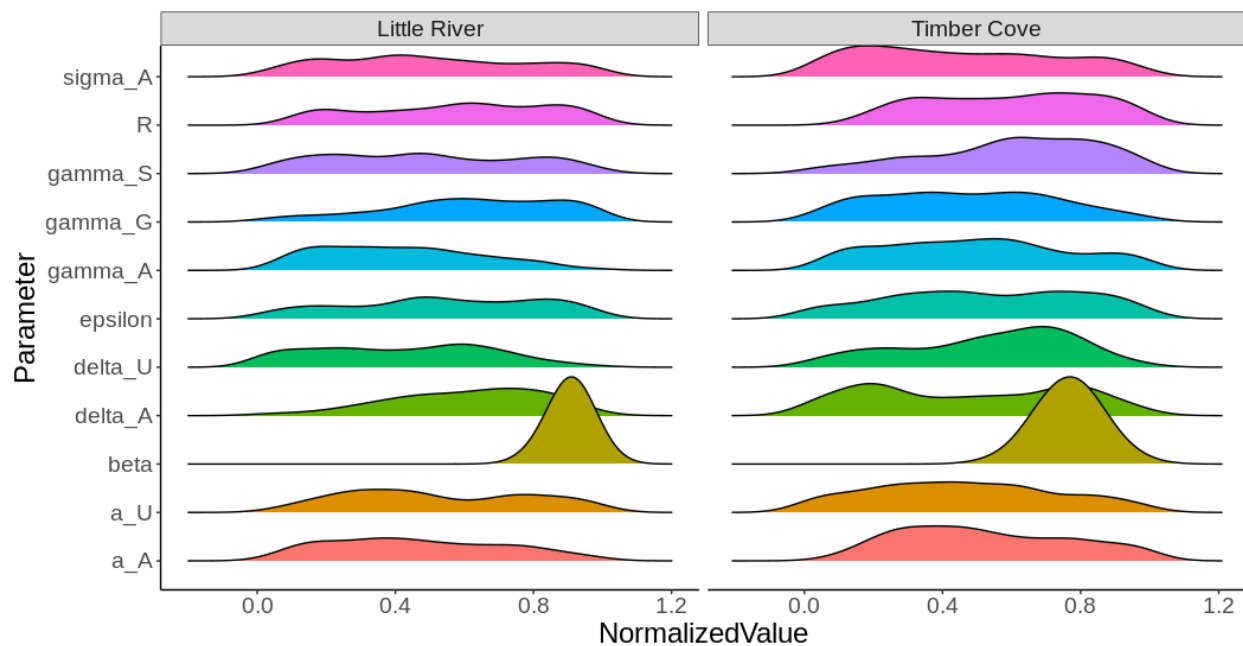


FIGURE F.1. Posterior distributions obtained using the Approximate Bayesian Computation algorithm for each of the parameters for both the Little River and Timber Cove regions. Notice that β is estimated using a different approach (see main text).

APPENDIX G

Spread rates 4.1 at different values of kelp mean dispersal distance

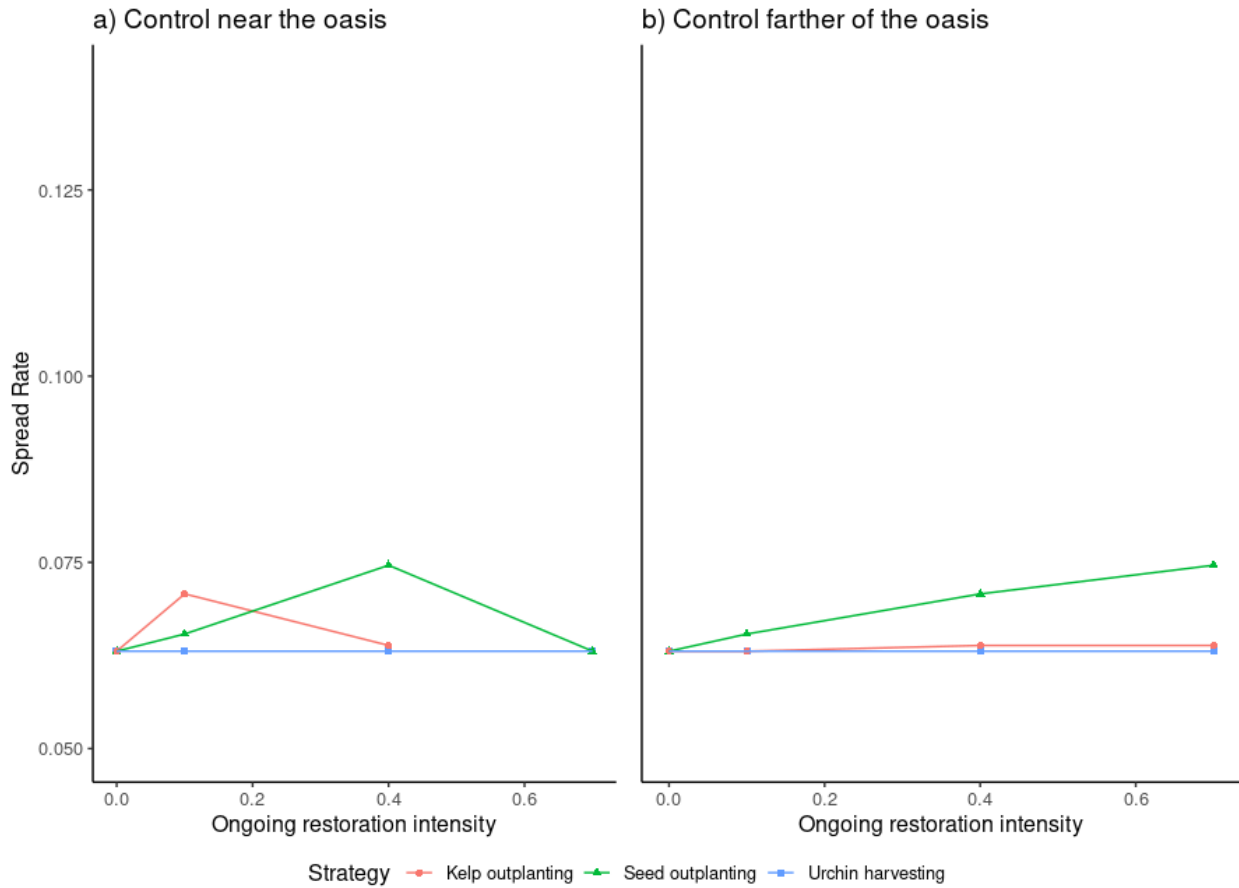


FIGURE G.1. Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below the threshold value necessary for kelp recovery and with an initial kelp density $2/\beta$ and half the estimated mean dispersal distance (double the baseline of a_A). Each line represents a different strategy: kelp outplanting in red circles, kelp seeding in green triangles, and sustained urchin harvest in blue squares. Panel a) shows ongoing restoration efforts near the kelp oasis ($\eta = 1$), and panel b) shows ongoing restoration efforts across a wider region of the coastline ($\eta = 10$). Compare to Fig. 4.6b

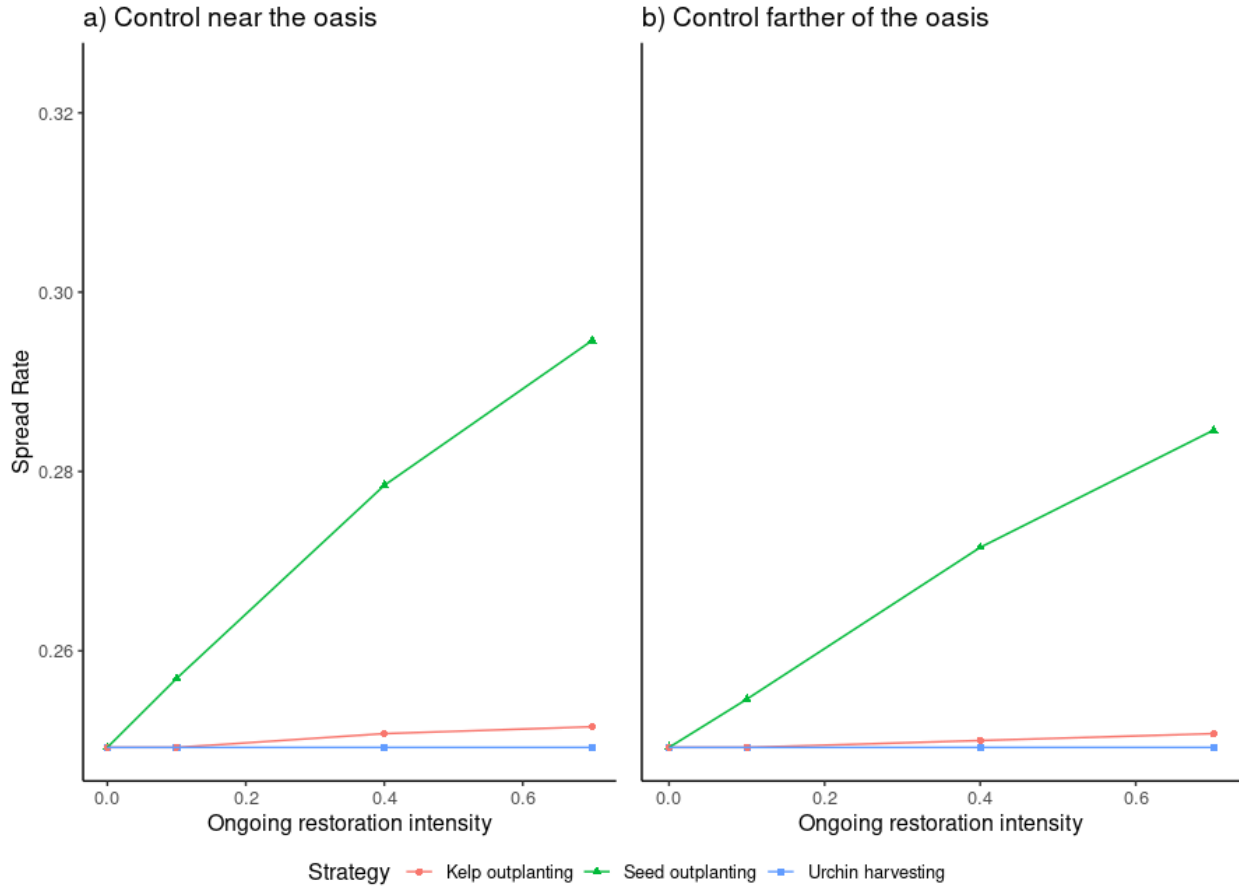


FIGURE G.2. Kelp spread rate under different restoration strategies with increasing intensity following urchin removal below the threshold value necessary for kelp recovery and with an initial kelp density $2/\beta$ and double the estimated mean dispersal distance (half the baseline value of a_A). Each line represents a different strategy: kelp outplanting in red circles, kelp seeding in green triangles, and sustained urchin harvest in blue squares. Panel a) shows ongoing restoration efforts near the kelp oasis ($\eta = 1$), and panel b) shows ongoing restoration efforts across a wider region of the coastline ($\eta = 10$). Compare to Fig. 4.6b

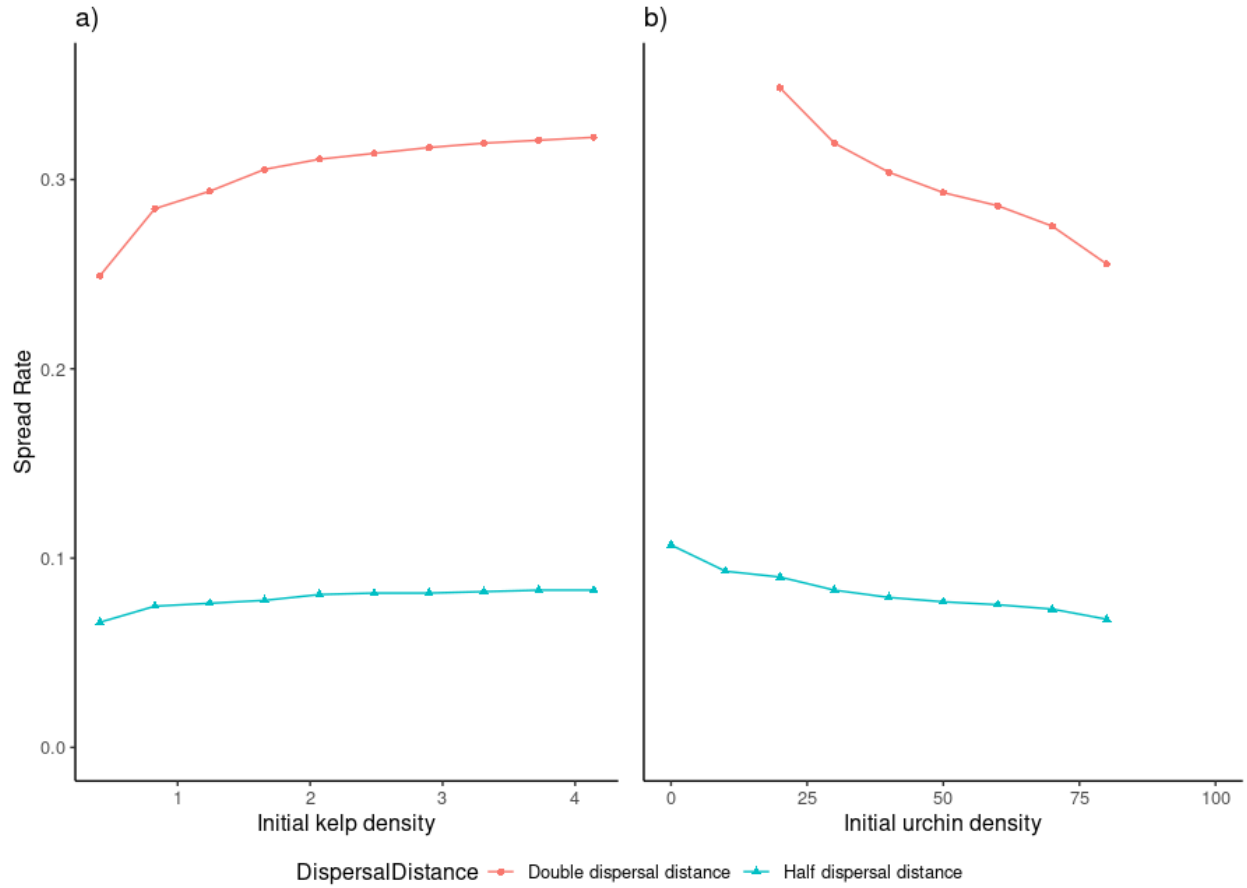


FIGURE G.3. Kelp spread rate under different initial conditions for partial restoration efforts at the initial (short-term) restoration stage. Each line represents a different value of mean dispersal distance, either double or half mean dispersal distance from the baseline. Panel a) shows the change in spread rate as the initial kelp density varies, and panel b) shows the change in spread rate as the initial urchin density varies.

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