

# The role of environmental stochasticity in driving ecological and evolutionary dynamics

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## Committee

- Chair: Sebastian Schreiber
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## Outline

- Background on environmental stochasticity and management
- Shortened version of seasonality review paper
- Shortened version of evolution of reproductive timing manuscript
- Main focus on my proposed chapters
  - Marine protected area design with rare events
  - Sea star wasting disease
- References

## 1 Introduction

2 Variability in environmental conditions is ubiquitous in nature. Writing on exponential growth in human  
3 populations, Malthus (1798) recognized that other factors should slow this growth:

4 

"...of many interrupting causes, such as the introduction or failure of certain manufactures,  
a greater or less prevalent spirit of agricultural enterprise, years of plenty, or years of  
scarcity, wars and pestilence, poor laws..."

5 Malthus is hitting on key factors of environmental variability for human populations. Later, Hutchinson  
6 (1961) examined the role of environmental variability in allowing many similar species to coexist when they  
7 would otherwise go extinct. Environmental variability is one of the structuring features of all ecological  
8 systems (Boyce et al. 2006, Lawson et al. 2015). Lande et al. (2003) argue that demographic and  
9 environmental stochasticity is far more important in determining population variability compared to internal  
10 cycles or chaos.

11 Here I do not distinguish between natural and anthropogenic factors and consider both as environmental  
12 variability. This type of variability is typically thought of as an "outside force" affecting the study  
13 system. Demographic stochasticity would be variability driven by internal dynamics, like births and

deaths, especially in small populations (Lande et al. 2003, Melbourne and Hastings 2008). Conversely, environmental stochasticity would include other abiotic or biotic factors that may affect many individuals of that population similarly (Lande et al. 2003). For my purposes environmental factors may include temperature, precipitation, snowfall, other species, and infectious diseases. In addition, factors such as oil spills, nutrient runoffs, hurricanes are also important. Further, many forms of variability, like resource pulses, can create benefits for species and communities (Yang et al. 2008). Environmental variability can affect demographic parameters (i.e. vital rates) for particular species (Lawson et al. 2015). In turn this has consequences for whole communities and ecosystems, and how we manage these systems. In addition to ecological dynamics, species have evolved a myriad of strategies to handle environmental variability, like bet-hedging and long lifespans (Childs et al. 2010).

Typically, people model environmental stochasticity by adding stochastic elements to deterministic model skeletons (Lawson et al. 2015). In contrast to deterministic models, stochasticity allows for population extinction. Lewontin and Cohen (1969) examined simple exponential growth models where  $R(t)$  in  $N(t+1) = R(t)N(t)$  was allowed to vary for each time step  $t$ . More specifically, values of  $R(t)$  were drawn from a Gaussian distribution. They found that the geometric mean, as opposed to the arithmetic mean, of  $R(t)$  determined extinction risk in the future. This is related to the general idea of Jensen's inequality, which explains why the mean of a function after certain transformations is different than transforming the mean of the function. In a series of papers, Tuljapurkar explored the role of environmental variability in population dynamics. He was specifically interested in structured populations where vital rates varied from one time step to the next. He extended Lewontin and Cohen (1969) to structured populations and found approximations to the stochastic growth rate when variability was small (Tuljapurkar 1990). Lawson et al. (2015) reviewed the importance of including environmental stochasticity in studies of ecology and the available mathematical tools. They stress that environmental stochasticity can cause increases or decreases in longterm growth rate. They also point out that not accounting for environmental stochasticity in population models can change, or even reverse, conclusions on species responses to environmental change (Lawson et al. 2015). There are many characteristics of environmental variability that determine their effect on ecological systems. Moving beyond simple Gaussian noise, other distributions or empirical data can be used. In addition, various characteristics of noise (e.g. tails of distribution, autocorrelation, magnitude, frequency) affect how vital rates and thus populations are affected (Lande et al. 2003, Schreiber SJ 2010).

Concurrently with changes in mean values of many environmental factors, variability in those factors is also expected to change in many systems (Vázquez et al. 2015). For instance, climate change is expected to change variability in temperature and precipitation (Vázquez et al. 2015). McLaughlin et al. (2002) used a set of models and field data to demonstrate that increased variability in precipitation led to the extinction of two populations of a checkspot butterfly. Further, climate change is expected to change the frequency and magnitude of tropical storms, flooding events, and heat waves (Smith 2011). These types of rare events may happen infrequently, but they can have disproportionately large effects on ecosystems. For instance, in systems with alternative stable states, large perturbations can move a system from one state to another (Scheffer et al. 2001). In the context of evolutionary dynamics, large environmental variability also presents strong selective pressures for organisms. For example, droughts present the Galapagos finch with strong selection on beak size (Boag and Grant 1981).

In this proposal, I describe four separate projects threaded together by the influence of environmental stochasticity. I will briefly describe chapters 1 and 2 as both are largely finished and in preparation for submission. Chapter 1 is a review paper on the role of seasonality in ecology. I describe different approaches for modeling seasonality and how seasonality is a structuring component in many systems. In chapter 2, I describe a modeling project on the evolution of reproductive timing. I built a general model of phenology evolution and then applied it to study the evolution of reproductive timing in the collared pika *Ochotona collaris*. Chapters 3 and 4 are distinctly different from the first two. In chapter 3, I describe a general model for how to design marine protected areas in the face of uncertainty, particularly rare events (Halpern et al. 2006). I discuss applications to coral reefs in the Caribbean. In chapter 4, I examine how environmental

63 variability (particularly in temperature) affects disease dynamics in sea stars. I will use a simple set of  
64 mathematical models parameterized with field and lab data to understand future disease risks under climate  
65 change.

## 66 1 Review paper on seasonality in ecological systems

67 Easton R White, Alan Hastings, in prep for *Ecology Letters*

### 68 1.1 Introduction

69 Seasonality is a nearly ubiquitous feature of ecological systems since in essentially all environments climatic  
70 drivers are seasonal. Here, we define an environmental variable as seasonal if it experiences regular, roughly  
71 periodic changes on an annual basis. Seasonal variables relevant in ecological systems include rainfall,  
72 temperature, photoperiod, wind, human activity, upwelling, and resource pulses. Seasonal factors are  
73 difficult to study. From an empirical perspective, data must be collected throughout the year, over several  
74 years to understand the role of seasonality in ecological systems. Ignorance also stems from the lack of  
75 tools ecologists have mathematically to deal with seasonal factors. Mathematical models of populations or  
76 communities are much more difficult to solve with the addition of seasonal forcing terms.

77 In this review, we explore a number of different areas of ecology that seasonal factors have been found  
78 to be important, or where incorporating seasonal dynamics may enrich our current understanding. We  
79 introduce some of the theory available regarding seasonal dynamics and how it relates to single-species,  
80 community, and ecosystem dynamics. In addition, we discuss a number of key areas like disease dynamics  
81 or animal migrations where the inclusion of seasonal factors is essential. Lastly, we discuss implications of  
82 seasonality for management and conservation issues in a changing world. The current version here is an  
83 abridged version of a manuscript in preparation for submission to *Ecology Letters* this year.

### 84 1.2 Theory for seasonality

85 Including seasonal components to standard population models can alter predictions of those models. For  
86 instance in a pair of differential equations, with seasonal forcing terms, periodicity and even chaos can  
87 appear; the forcing terms essentially act to increase the system dimension.

88 In standard population models, we have several techniques that are often employed to learn about their  
89 dynamics: equilibrium and stability analyses, phase plane diagrams, and finding solutions in simple cases  
90 in some cases. However, modeling seasonality presents additional challenges. A simple approach would  
91 be to include periodic forcing terms in models. Models of this form can sometimes be analyzed with  
92 Floquet theory (Klausmeier 2008), but numerical methods may be needed. Depending on the specific role  
93 of seasonality and questions asked several other mathematical approaches may be relevant: nonautonomous  
94 equations, successional state dynamics (Klausmeier 2010), impulsive differential equations, hybrid models,  
95 or simulations.

### 96 1.3 Empirical examples of seasonality

97 In our manuscript in preparation, we detail sections for various examples of seasonal variability in natural  
98 systems. Here I present a single bullet point for each section.

- Disease dynamics: There are several well-known examples where seasonality has been identified as a key factor in understanding infectious diseases of both humans and animals. Seasonality can affect host behavior, modify host immune responses, alter encounter rates between pathogens and hosts, and affect the biology of disease vectors via changing season lengths and magnitude (Altizer et al. 2006). One textbook example in epidemiology is the outbreak of the contagious childhood disease measles in England (Grenfell et al. 2001). Models with the inclusion of seasonal factors accurately predict sustained, large amplitude cycles (Grenfell et al. 2001).
- Animal migrations: Animal migrations both on land and in the sea have long fascinated ecologists. The timing of migration is ultimately a phenological phenomenon. Photoperiod is a reliable cue used by both migratory and resident individuals. However, temperature, precipitation, or rhythmic cycles may also be used (Dingle 2014). Different species use different cues, or respond differently to changing cues. Perhaps not surprisingly, with global climate change, some migration cues are becoming unreliable or species are not responding to changes in climate.
- Species interactions: Types of species interactions may include competition, predation, parasitism, mutualism, as well as many others. Early work focused on how two species can coexist given limited resources (Ayala et al. 1973). Seasonal factors can promote temporal niche partitioning. In addition to competition, a lot of work has examined predator-prey interactions in relation to seasonal forcing. Taylor et al. (2013) examined a simple predator-prey model forced with seasonal terms and found multi-year cycles, quasi-periodicity, and chaos are all possible. Recently, McMeans et al. (2015) argued that temporally forced food webs are the norm in ecology and that including temporal variability in models has an effect on both ecosystem function and stability.
- Seasonality and global change: It has become clear that the phenology of many plant and animal species has advanced due to anthropomorphic climate change (Visser and Both 2005). Shifts in the timing of these events can be driven by changes in temperature, precipitation, or extreme weather events (Smith 2011). Global climate change can alter the phenology of species in primarily three ways: mismatch in the timing of seasonal events, increased or decreased season lengths, and lastly, a reduction or increase in the seasonal variability. The specific mode in which climate change affects seasonality can have important effects for ecological dynamics. In response to climate change, a species can adapt (through phenotypic plasticity or genetic adaptation), move, or go extinct (Reed et al. 2011).

## 1.4 Conclusion

Seasonality is a particular type of temporal variability and is ubiquitous in ecological systems. We presented several scenarios where an appreciation for seasonal forces is essential for ecological understanding, including species interactions, disease dynamics, and animal migrations. In response to climate change, there are numerous examples of changing phenologies of plant and animal species across the globe (Forrest and Miller-Rushing 2010). Empirically, an understanding of seasonal forcings requires long-term observations or experiments. Therefore, data from several years, including multiple seasons, are required to characterize such a system. Mathematically, we have few tools to handle large variability in even simple models. Of course, we have even fewer tools available in more complicated ecological systems (McMeans et al. 2015). In general, we believe seasonality, and its effects on ecological systems, are under-appreciated. Further, an understanding of seasonal forces will become increasingly important in the context of global change.

## 2 Opposing selective pressures on reproductive timing in the face of climate change

Easton R White, Kalle Parvinen, and Ulf Dieckmann, in prep. for *Evolutionary Applications*

### 2.1 Introduction

For many species their seasonal timing of life history events, or phenology, is important for both ecological and evolutionary dynamics (Forrest and Miller-Rushing 2010). Phenology includes the timing of migration, feeding, hibernation, mating, and reproduction. For example, reproductive timing is often restricted to certain parts of the year and depends on factors like snowfall, food availability, and predation pressures (Bronson 2009). Recent work has highlighted the importance of climate change in driving phenological shifts for a number of different species (Forrest and Miller-Rushing 2010). Of particular concern, are interacting species which may respond to different cues, or at least respond at different rates to the same cues (Johansson et al. 2015). In addition to changing the mean timing of spring onset, climate change is expected to alter the variability in timing of spring onset (ACIA 2005). This leads to the question of how phenological timing should evolve given a variable environment (Iwasa and Haccou 1994).

Both environmental variability and climate change are expected to be particularly relevant at higher latitudes, where seasonal selective pressures are strong (Stevenson et al. 2015). In addition, to build sophisticated models and to predict the effects of climate change, high-quality data must be available. One case study that fulfills both of these criteria is the the collared pika (*Ochotona collaris*) found in the Yukon, Canada. In recent years, concerns have developed about the effect of climate change on pikas (COSEWIC 2011, but see Smith and Nagy 2015). The collared pika was recently listed as a species of concern by Canada, because of the potential effect of climate change on their populations in the near future (COSEWIC 2011).

We have three primary aims: 1) to build a general model of phenology evolution that accounts for eco-evolutionary dynamics and environmental factors, 2) to investigate the role of environmental variability in driving evolutionary dynamics, and lastly 3) to explore how changes in mean timing, in addition to the variability in timing, of spring affect evolutionary dynamics under projections of climate change. To account for realistic ecological dynamics and environmental factors, evolutionary game theory is appropriate. Our general modeling framework incorporates physiology, population dynamics, and environmental factors to examine the evolution of reproductive timing. As a case study, we apply our model to a population of collared pika found in Ruby Ridge, Yukon, Canada (Franken and Hik 2004b, COSEWIC 2011). Of particular interest for pikas at this site is the prediction that climate change will induce an earlier onset of spring and the onset of spring will be more variable on a year-to-year basis (ACIA 2005).

### 2.2 Methods

We are interested in organisms that have a specific window of the year in which they can reproduce, the reproductive season. A reasonable framework for this type of system is a coupled set of differential equations and a discrete-time map, a hybrid model. More specifically, we model within-reproductive season dynamics as a continuous process (within-season dynamics) and map from one year to the next (between-season dynamics). Within-season dynamics are modeled with a set of ordinary differential equations that track population density for different life stages, their respective resource reserves, resource density, and the environment.

### 2.2.1 Model

We explicitly model the snow depth ( $E(t)$ ), adult density ( $A(t)$ ), juvenile density ( $J(t)$ ), adult haypile size ( $B_A(t)$ ), juvenile haypile size ( $B_J(t)$ ), and the plant biomass ( $R(t)$ ). We assume a birth pulse reproductive strategy where all reproduction occurs at a single instance.

$$\begin{aligned}
\text{Snow depth:} & \quad \frac{d}{dt}E(t) &= eE(t), \\
\text{Adult density:} & \quad \frac{d}{dt}A(t) &= -u_A A(t), \\
\text{Juvenile density:} & \quad \frac{d}{dt}J(t) &= -(u_J + u_E \frac{E(t)}{K+E(t)})J(t), \\
\text{Adult haypile size:} & \quad \frac{d}{dt}B_A(t) &= w_A \frac{a_A R(t)}{1+a_A h_A R(t)} - \beta_A B_A(t), \\
\text{Juvenile haypile size:} & \quad \frac{d}{dt}B_J(t, \tau) &= w_J \frac{a_J R(t)}{1+a_J h_J R(t)} - \beta_J B_J(t), \\
\text{Plant biomass:} & \quad \frac{d}{dt}R(t) &= rR(t)(1 - \frac{R(t)}{K_R}) - A(t) \frac{a_A R(t)}{1+a_A h_A R(t)} - J(t) \frac{a_J R(t)}{1+a_J h_J R(t)}
\end{aligned} \tag{1}$$

Here  $E(t)$  decays at a rate  $e$  through the course of the season. Both  $A(t)$  and  $J(t)$  decrease during the course of the season according to specific mortality rates. The juvenile summer mortality rate depends on  $E(t)$  and three parameters:  $u_J$  (mortality rate when no snow is present),  $u_E$  the maximum mortality rate from snow, and  $K$  (a half-saturation constant). We assume a Holling type II (or type I if  $h = 0$ ) functional response for resource acquisition which includes handling time  $h$  and an attack rate  $a$ . The resources reserve also decays at a rate  $\beta$ . Lastly, the plant biomass is assumed to exhibit logistic growth.

The birth of new juveniles  $J(\tau) = \alpha A(\tau)$  occur during the reproductive season with a new cohort of juvenile at time  $\tau$  (a birth pulse with rate  $\alpha$ ). As in many species, we do not know which cues pikas use to time reproduction. Therefore, we investigate two different reproductive strategies: 1) timing cue – this is a cue based on the timing within year, like photoperiod and 2) environmental cue – this cue depends on an environmental factor, like snow depth. For the environmental cue, the strategy value is the threshold of snow depth at which pikas will begin reproducing.

The between season dynamics provide the initial conditions for the differential equations used for within season dynamics. The environment, snow depth, initial condition,  $E(0)$ , is given by a random variable. For pikas, we assume that juveniles mature and become adults after their first winter. Adult pika initial density is given by the number of surviving adults and juveniles from the previous year, which also depends on their respective haypile size. Because of data limitations, we assume adults and juveniles have the same parameter values; this assumption may be important, particularly in the case of phenology (Yang and Rudolf 2010).

### 2.2.2 Case study of the collared pika

We apply our model to a population of the collared pika (*Ochotona collaris*) located in the Ruby Ridge Mountains, Yukon Territory (61° 12' N, 138° 16' W; 1800-2000m). Since 1995, pikas have been live-trapped and given unique identifying tags (Franken and Hik 2004b). More information on the specific data collection methods is given in Franken and Hik (2004b). Importantly, several studies have collected detailed life-history information needed to parameterize our model. Starting from a general model, we made several specific model specifications for the collared pika (see Manuscript for details).

## 2.3 Results

We evaluated two types of reproductive strategy types in our analyses. Here we focus on the cue based on the amount of snowfall as that is more interesting in stochastic settings, particularly with climate change. In the main manuscript, we present additional results.

### 2.3.1 Selective pressures under climate change

In many areas, climate change is predicted to have two main effects on the timing of spring (ACIA 2005). Climate change is expected to cause an earlier timing of the onset of spring (which refers to a lower  $E(0)$  in our model). In addition, climate change is expected to cause a more variable timing of the onset of spring (an increase in  $var(E(0))$ ). To test effects of these predictions, we explored different mean and variances of the environmental initial condition and determined the predicted evolutionary stable strategies (Fig. 1). Here, selection for a lower tolerance to snow occurs for decreasing values of the environmental initial condition (Fig. 1a). In addition, there is selection for a delayed timing of reproduction with increasing variability in the environmental initial condition (Fig. 1c).

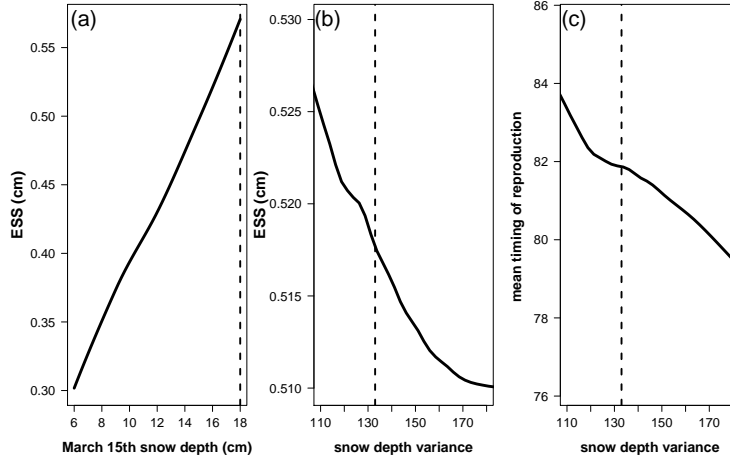


Figure 1: Relationship between predicted evolutionary stable strategy and  $E(0)$  or variability in  $E(0)$ : a) ESS for different values of  $E(0)$  while holding  $var(E(0))$  constant, b) ESS for different values of  $var(E(0))$  while holding  $E(0)$  constant, and c) Mean reproductive timing for different values of  $var(E(0))$  while holding  $E(0)$  constant. The three vertical dashed lines indicate the historical values for the Yukon study site.

## 2.4 Discussion

We began by building general eco-evolutionary framework (not shown in the proposal) that incorporates stage structure, physiology, and environmental variables. The model is flexible enough to be applied to many different populations of plants or animals. As a case study, we applied our model to a population of the collared pika in the Yukon (Franken and Hik 2004a). With a parameterized model of population dynamics we were able to examine the evolutionarily stable strategy for reproductive timing. We examined two different cues: a timing cue, based on timing within the year; and an environmental cue, where timing is based on the amount of snow present at any given time. For both cues, our model predicts an interior evolutionarily stable strategy where reproduction occurs in the middle of summer, as opposed to the beginning or end of summer (Eskola 2009). For the environment-based cue, pikas have an ESS of 0.54cm, which corresponds to an average date of reproduction in mid-June. At the Yukon site, pikas, on average, reproduce on June 18th, but this varies between June 5th and July 2nd (Franken and Hik 2004b). This strongly suggests pikas use a cue based on environmental conditions (Franken and Hik 2004b).

In the Yukon, along with many other areas, climate change is expected to have two main effects on seasonal timing. First, and most commonly discussed, is the earlier timing of spring and the subsequent earlier timing of biological activity. Secondly, climate change is expected to increase the variability in timing of spring onset (ACIA 2005). As we have demonstrated, these two predictions of climate change models may have conflicting selective pressures. The effects of climate change on pikas will depend on the exact

quantitative relationship between the mean timing of spring onset and the variability in timing. Further, fitness benefits or costs will depend on how pikas are able to respond to these changing factors.

Our work demonstrates the existence of conflicting selective pressures for phenological timing under future climate change scenarios. There has been a lot of literature documenting earlier timing of reproduction driven by climate change (Forrest and Miller-Rushing 2010), but less work on the role of increased variability in climatic factors (Smith 2011). Lastly, our work provides some insight into a species that may already be affected by climate change (COSEWIC 2011).

### 3 Designing marine reserves for resilience to extreme events

Easton R White

#### 3.1 Introduction

In marine systems there are often several, seemingly conflicting management goals including fisheries, conservation, and economic development (Botsford et al. 1997, Gaines et al. 2010). To overcome conflicting management goals, ecosystem-based management (as opposed to managing resources in isolation) has been advocated as a more holistic approach. Recently, marine protected areas (MPAs) have emerged as one type of ecosystem-based management strategy (Gaines et al. 2010). Current international agreements (e.g. Sustainable Development Goals) aim for 10% of coastal and marine areas to be set aside by the year 2020. Many countries have responded with developments of their own marine protected area plans. There is a rich set of theory on how to design marine protected areas and in particular networks of MPAs (Botsford et al. 2001, Hastings and Botsford 2003; 2006, Gerber et al. 2003, Fulton et al. 2015). Many factors contribute to the potential success of marine protected areas: MPA size, connectivity between MPAs, species life history (e.g. reproductive output, dispersal distance), fishing management outside reserves, and enforcement. Importantly, marine reserves are expected to not only change population dynamics, but also community level processes (Baskett and Barnett 2015).

There have been two general approaches to MPA planning: static optimization and dynamic (often bioeconomic) modeling (Fulton et al. 2015). Static models include information on habitat and species distributions coupled with economic factors (e.g. fisheries) to identify optimal locations and sizes of marine reserves (Game et al. 2008). These models can usually be implemented quickly and have less data requirements. At the other end of the spectrum are dynamic modeling approaches which focus more on population dynamics and connectivity between areas. Necessarily, these models require more detailed demographic information and reserve planning optimization routines require more time (White et al. 2014).

Most MPA planning does not account for environmental variability (but see Mangel 2000, Halpern et al. 2006, McGilliard et al. 2011). In theory, environmental variability should increase the amount of protected area needed to achieve conservation or management goals (Allison et al. 2003), although this strongly depends on the spatial structure of the population (McGilliard et al. 2011). The effects of environmental variability manifest in ways specific to individual species (e.g. reproductive output, survival). Further, these effects of environmental variability are usually differentially expressed spatially: local or global effects. In addition to environmental variability in general, even less work has examined the role of infrequent, or rare, events Smith (2011). Although rare, these types of events can be particularly devastating to marine ecosystems (McGilliard et al. 2011, Fabina et al. 2015). By their very nature, these types of events are difficult to study. For example, Game et al. (2008) used a static optimization approach to determine the effect of accounting for rare bleaching events in the Great Barrier Reef. Their approach included bleaching risk as a model constraint that tries to preserve different bioregions. However, a dynamic modeling approach



is needed to truly evaluate the role of environmental stochasticity as static approaches can only do this in an ad hoc fashion.

I have three primary aims in this chapter:

1. Build a general model of marine reserve design that allows for environmental stochasticity, including rare events
2. Estimate and describe the distributions of rare events in a spatially-explicit context
3. Apply models to a coral reef system in the Caribbean (Mumby et al. 2011)

I will describe current methods of marine reserve design and how I plan to build on that work. I will then examine various approaches to studying rare events. Lastly, I describe a specific system where my approach is applicable.

## 3.2 Methods

In the past two decades, many spatial planning tools have emerged (Fulton et al. 2015). MARXAN is among the most popular for its ease of use and low data requirements. Essentially, MARXAN uses optimization techniques (simulated annealing) to determine locations and sizes of marine reserves given some spatial data on species distributions. The program is able to include constraints like costs and conservation or fishery goals. One major drawback of MARXAN is the lack of specific ecological detail, like connectivity. Recently, White et al. (2014) (not me unfortunately) included larval connectivity in these bioeconomic models like MARXAN. They found that including connectivity was essential for meeting targets for some species, depending on their biology.

Including this type of demography in models is important as environmental variability affects populations through resulting changes in their demographic parameters, or vital rates. In order to study the role of uncertainty in marine spatial planning, I propose extending the model of White et al. (2014) to include stochastic dynamics so environmental variability can be readily included.

### 3.2.1 Aim 1: Model of marine reserve design that accounts for rare events

I will use a discrete-time, spatially explicit population model which can allow for age structure (White et al. 2014). Connectivity between spatial locations is given by a dispersal matrix  $D_{ij}$ , where the entry  $i, j$  indicates movement of individuals from location  $j$  to  $i$ . Therefore the total number of immigrants to population  $i$  at time  $t$  is  $S_i(t, E(t)) = \sum_{j=1}^n D_{ij}(E(t))N_j(t)$ .

$$N_i(t+1) = g(N_i(t), E_i(t)) + s(N_i(t), E_i(t)) \cdot N_i(t) + S_i(t, E(t)) \quad (2)$$

$$E_i(t+1) = f(E_i(t)) \quad (3)$$

The population within one patch (or population within a metapopulation) is given by dispersal ( $S_i$ ), local population growth ( $g(\cdot)$ ), and survival of individuals ( $s(\cdot)$ ) from  $t$  to  $t+1$ .

Unlike past work (White et al. 2014), this model is allowed to have stochastic variables.  $E_i(t)$  describes the environment at time  $t$ . This could be a vector with variables for temperature, acidity, or other relevant parameters. Depending on the specific system, environmental stochasticity can arise in several ways to affect dispersal, survival, and reproductive output.

### 3.2.2 Aim 2: Estimating frequency of rare events

Rare events, due to their rareness, are by their very nature difficult to study (Mangel and Tier 1994). The frequency of rare events of course depends on the spatial and temporal scales evaluated. Like all environmental variability, there are various properties of rare events that are important, including: magnitude, duration, frequency, and predictability. There are generally three approaches to model rare events.

1. With sufficient data, distributions of the frequency and magnitude of rare events can be constructed
2. In the absence of sufficient data, distributions (like a power law) can be assumed and their parameters can then be estimated
3. Mechanistic models where rare events would be an emergent property (e.g. global climate models and bleaching risk in corals)

### 3.2.3 Aim 3: Application to corals in the Caribbean

In marine settings, environmental stochasticity, and specifically rare events, can take many forms. Detailed mechanisms of how environmental stochasticity actually affects organisms should be known (Baskett 2012).

Recently, (Mumby et al. 2011) described a static approach (using MARXAN) to create a marine reserve network in the Caribbean. They were specifically interested in designing a marine reserve network that would allow corals to be resilient to changes in climate, and therefore increased temperatures and risks of bleaching. They included a simple cost function in their MARXAN model to prioritize connectivity between coral reefs. However, they needed to make simplifying assumptions about the biology of coral reefs, community structure, and human influences. A dynamic modeling approach is required to account for this complexity and to determine robust marine reserve networks, not only in the context of climate change, but also risks from hurricanes and fishing activity.

I will use the spatially structured, stochastic approach described earlier to model coral reef dynamics. Importantly, oceanographic models provide data on connectivity between sites (Fig. 2). In addition, data exists on bleaching risk for different sites and hurricane tracks in the area (Fig. 2). I will use projections of bleaching risk and hurricane activity estimated until 2100. With a working model of the population dynamics of coral reefs in a stochastic environment, I can then explore different reserve network designs. Eventually, a “optimal” configuration of marine reserves may be found. I will compare this configuration to situations where catastrophe risks are not taken into account and to the results from (Mumby et al. 2011).

## 3.3 Potential results

Including environmental stochasticity, and in particular rare events, has the potential to alter the design of marine protected areas (Allison et al. 2003, Game et al. 2008). With increased stochasticity, a diversity of marine protected areas provides redundancy. This is

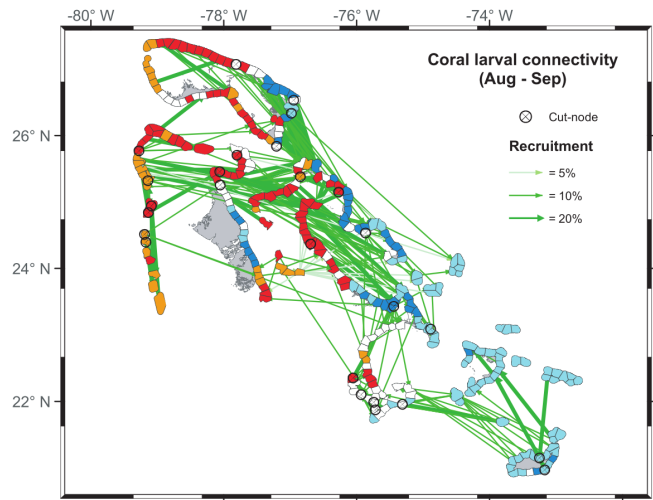


Figure 2: Connectivity between coral reefs in the Caribbean based on oceanographic models. Colors represent different types of coral reefs (in regards to their susceptibility to bleaching).

359 especially true when environmental stochasticity is correlated in space. Static optimization routines cannot  
 360 truly examine how environmental stochasticity affects marine systems as they lack biological mechanisms.

361 It is also important to consider the role of multiple disturbances in marine reserve design (Mellin et al.  
 362 2016). Disturbances can act differently in terms of their effects on ecological systems via varying disturbance  
 363 frequency, magnitudes, or their spatial extent. Bleaching, hurricanes, and fishing all present different  
 364 challenges for coral reef resiliency and spatial planning.

## 365 4 Modeling seastar wasting disease

### 366 4.1 Introduction

367 Throughout the world’s oceans, there has been increasing concern regarding extreme temperatures and  
 368 their effect on coral reefs, kelp, seagrasses, and other important ecosystems. Historically, these systems  
 369 have evolved to handle certain amounts of environmental variability. However with climate change, extreme  
 370 summer temperatures are expected to happen more frequently and for longer durations (Smith 2011). It is  
 371 unclear if corals will be able to adapt quickly enough to overcome the harmful effects of bleaching.

372 Sea stars are keystone predators in the rocky intertidal (Paine 1966). The losses of sea stars can lead to  
 373 community-level effects. As keystone predators many sea star species create space in the intertidal which  
 374 increases local diversity (Paine 1966). In June 2013, began a massive die-off of sea stars (Class Asteroidea)  
 375 on the west coast of North America. Sea star wasting disease, a catch-all term, causes lesions and eventual  
 376 death for sea stars (Hewson et al. 2014). The disease has been identified in 20 species of sea stars from  
 377 Baja California to Alaska. Biomass of sea stars in some areas declined up to 90% because of the disease  
 378 (Menge et al. 2016).

379 The disease is still poorly described, but a densovirus (Parvoviridae) is now implicated as the cause (Hewson  
 380 et al. 2014). The virus is found in the tissues of symptomatic sea stars, in the water column, and in  
 381 sediment (Hewson et al. 2014) Like other diseases, sea star wasting disease (via transmission and infection  
 382 load) is also associated with warmer water temperatures (Eisenlord et al. 2016). In the Northeast Pacific,  
 383 warmer waters occurred largely because of El Nino activity (Eisenlord et al. 2016); sustained heatwaves of  
 384 potentially larger magnitude may be more common because of climate change.

385 I plan to develop simple mathematical models parameterized with field and lab data to address four  
 386 questions:

- 387 1. Can a simple mathematical model explain the interaction between temperature and disease in  
 388 contributing to the current dieoff of sea stars?
- 389 2. Which areas will a high risk of disease in the future?
- 390 3. What management actions (e.g. culling) could be taken once an outbreak was identified?
- 391 4. How would you design marine reserves to promote conservation of sea stars in the absence versus  
 392 presence of the disease?

### 393 4.2 Methods

#### 394 4.2.1 Simple models

395 Sokolow et al. (2009) examined a general metapopulation model of infectious marine diseases. Their model  
 396 was spatially implicit and differed from most disease models as it included a free-living pathogen. They

397 applied their model to a recent white plague outbreak among coral in the Florida Keys. I will modify their  
 398 modeling framework to be suitable for sea star wasting disease (Fig. 3).

399 Based on the biology of the Densovirus associated and sea star life cycles, here is a simple schematic of  
 400 local populations dynamics (Fig. 3). The boxes in this figures would be connected to other boxes of local  
 401 populations dynamics.

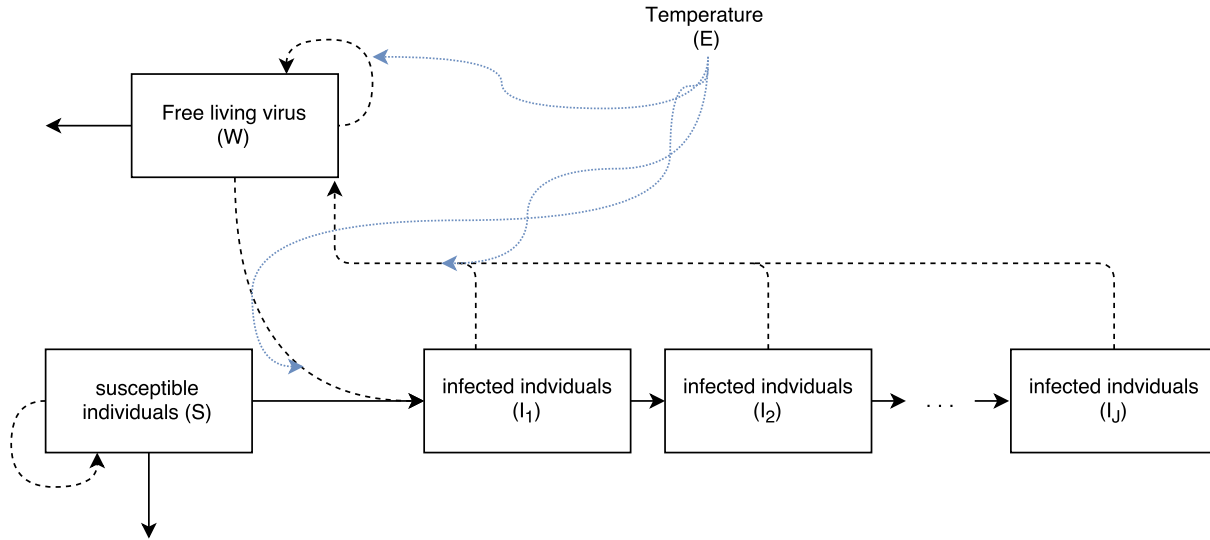


Figure 3: Simple SI model with a free-living virus stage, susceptible sea stars, and infected sea stars of different virus loads denoted by a subscript. Temperature affects several of the processes. The diagram represents a single population that could be connected to other populations via dispersal.

402 The model includes a free living virus ( $W$ ), susceptible sea star stage ( $S$ ), and several infected individuals  
 403 stages ( $I_j$ ), depending on viral load. Viral load and species differences (or host heterogeneity more  
 404 generally) may change predictions of these models (Lloyd-Smith et al. 2005). In addition, environmental  
 405 factors, specifically temperature, are known to affect various processes (Eisenlord et al. 2016).

#### 406 4.2.2 Data

407 There is data available from laboratory experiments and field observations. Eisenlord et al. (2016) examined  
 408 the role of temperature and size on the probability of disease in several species of sea star. In addition,  
 409 they documented time to death once a sea star became symptomatic.

410 Along the west coast, the University of California, Santa Cruz (in collaboration with partners) has maintained  
 411 longterm census records on intertidal organisms for the past several decades. In addition, many locations  
 412 have collected prevalence of seastar wasting disease.

#### 413 4.3 Possible results

414 A simple disease model with environmental variability should be able to describe the disease dynamics well.  
 415 If not, then the disease may be more complicated than what the model currently captures.

416 If temperature, sea star density, or both play a large role in outbreak dynamics then it may be possible  
 417 to predict which populations are the most likely to be susceptible in the future. For example, tracking  
 418 temperatures profiles may allow managers to predict outbreaks on a near-realtime basis (Lafferty and  
 419 Hofmann 2016). Managers could decide if culling or another strategy may be appropriate. In addition it is

important to understand if marine reserves will have benefits or costs in regards to the spread of diseases. Reserves can be a safe haven for diseased sea stars, but could also be important in repopulating areas affected by the disease.

## 5 PhD Timeline

Names	Spring 2016	Summer 2016	Fall 2016	Winter 2017
Chapter 1	Lit Review and writing		Finish writing	
Chapter 2	Lit review and writing	At IIASA	Finish writing	
Chapter 3			Lit review	Collect data
Chapter 4			Lit review	Disease course
	Spring 2017	Summer 2017	2017-2018	Summer 2018
Chapter 1				Defend
Chapter 2				Defend
Chapter 3	Modeling	Modeling	Analysis and writing	Defend
Chapter 4		Data and Modeling	Analysis and writing	Defend

## 6 Broader significance and future directions

Environmental variability is a ubiquitous feature of ecological systems. With climate change, and other anthropogenic drivers, environmental variability is expected to increase in many systems. My dissertation touches on how this type of environmental variability will affect seasonal dynamics, evolutionary dynamics, management of natural resources, and disease dynamics. My dissertation has a particular emphasis on the underappreciated effects of rare events in ecological systems (Smith 2011).

In the future, I would like to study other types of environmental variability in marine systems and how this may affect management decisions (Halpern et al. 2006). I think the most difficult empirical challenge moving forward is to obtain detailed enough information to model spatial processes, but to also be able to describe dynamics over large spatial scales.

The approaches I have described make a number of simplifying assumptions. In the future, it would be useful to study multi-species communities in marine reserve design (Baskett et al. 2007), other types of environmental stochasticity, and more detailed models of disease transmission.

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