Revisiting the logistic map: A closer look at the dynamics of a classic chaotic population model with ecologically realistic spatial structure and dispersal

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Abstract:

There is an ongoing debate about the applicability of chaotic and nonlinear models to ecological systems. Initial introduction of chaotic population models to the ecological literature was largely theoretical in nature and difficult to apply to real-world systems. Here, we build upon and expand prior work by performing an in-depth examination of the dynamical complexities of a spatially explicit chaotic population, within an ecologically applicable modeling framework. We pair a classic chaotic growth model (the logistic map) with explicit dispersal length scale and shape via a Gaussian dispersal kernel. Spatio-temporal heterogeneity is incorporated by applying stochastic perturbations throughout the spatial domain. We witness a variety of population dynamics dependent on the growth rate, dispersal distance, and domain size. Dispersal serves to eliminate chaotic population behavior for many of the parameter combinations tested. The model displays extreme sensitivity to changes in growth rate, dispersal distance, or domain size, but is robust to low-level stochastic population perturbations. Large and temporally consistent perturbations can lead to a change in population dynamics. Frequent switching occurs between chaotic/non-chaotic behaviors as dispersal distance, domain size, or growth rate increases. Small changes in these parameters are easy to imagine in real populations, and understanding or anticipating the abrupt resulting shifts in population dynamics is important for population management and conservation.

Keywords: Logistic map, spatial population model, spatiotemporal chaos, Gaussian kernel dispersal

Introduction:

Although the chaotic systems literature has grown over the past several decades, the bulk of it resides in the physical sciences (e.g. fluid dynamics) and is neither written for, nor read by ecologists. Early conceptual papers introduced chaotic concepts to the ecological literature (e.g., May 1973, May 1976, Schaffer 1985, Hastings 1993, Hastings et al. 1993) but computational limitations at the time restricted such research to simple models that are difficult to apply to real populations. Here, we revisit and build upon these earlier models by performing a closer examination of a chaotic population within an ecologically applicable framework. We create a chaotic growth-dispersal model with an explicit 1-dimensional spatial component, and detail dynamics for a large parameter space, examine the fractal-like boundaries between differing population dynamics regimes, and add stochastic elements to simulate spatio-temporal heterogeneity and observe the interactions between chaotic dynamics and stochasticity. In this way we add to the ecologists' chaotic toolbox by detailing the spectrum of behaviors possible for such a system. Incorporating enough ecologically realistic components insures that the model dynamics can be compared to the dynamics of real populations.

Chaos has been detected in many and diverse biological systems, such as the spread of infectious disease (Sugihara and May 1990), marine environments (Glaser et al. 2014), and plant growth dynamics (Billings et al. 2015). These studies focus on detection of chaos as a way to understand system stability and future behavior. There are few examples of directly modeled nonlinear populations, but Cushing et al. (2003) provide a thorough analysis of the nonlinear dynamics of the flour beetle, with both a nonlinear population model and actual experimental data to verify the model. We envision our

model as a stepping stone for further direct applications of nonlinear models to real populations, as our generalized model provides a mechanism for deeper understanding of the full range of dynamics present in a chaotic population, as well as a means of understanding the biological cause of behavioral changes in a population as ecologically relevant parameters change.

For example, harvesting of cod affects both the growth rate and dispersal of the population along its entire range. For cod in the Gulf of Maine, surplus production models illustrate how growth rates first increase (due to density dependence) to compensate for increased harvesting, and then decrease if the population is overfished. In heavily depleted, and therefore likely chaotic conditions (Glaser et al. 2014), the effects of this variability on cod dispersal (and, thus, availability to the fishery) is poorly understood and can result in management failures (NEFSC 55th SAW, 2013). For this reason, a better method for understanding changes in movement and dispersal in chaotic populations is essential to sustainable management.

The earliest introduction of chaotic population models to the ecological literature focused on zero-dimensional (zero spatial dimension, one-dimensional phase space) single-species models (May 1973, May 1976). Subsequent models added spatial dimension in the form of discrete patches, where a certain percentage of the population in one patch disperses to the adjacent patch(es) with each iteration of the model (Hastings 1993, Bascompte et al. 1992, Kaneko 1984, Willeboordse 2003, White and White 2005). When enough patches are incorporated, the model simulates a growth and diffusive dispersal system. However, such models employ numerical diffusion as a dispersal mechanism, which permits limited diffusion per iteration/generation, as the coupling

strength parameter must remain small for the validity of the system (Kaneko 1989). A subset of the literature expands the diffusive range by exploring globally coupled patches (Kaneko 1992, Sole et al. 1992, Willeboordse 2003, 2002), but these are limited to an even smaller portion of the population diffusing into neighboring patches, and each patch receives a uniform proportion of the population regardless of its proximity to the parent patch. Additionally, such models largely employ periodic boundary conditions, an ecologically unrealistic feature (Aiken & Navarrete 2014).

Improvements upon the numerical diffusion models were made when the diffusive dispersal mechanisms were replaced with dispersal kernels (e.g. Ruxton & Doebeli 1996, Doebeli & Ruxton 1998, Saravia et al. 2000, Labra et al. 2003). The kernels provide a more realistic dispersal scenario than discretized diffusion, as the dispersal distance is easily changed, and neighboring discrete locations generally receive a larger percentage of neighboring populations than far away locations.

Many of the aforementioned models share a common model of growth: the logistic map. The logistic map represents one of the simplest difference equations with chaotic dynamics, popularized by Robert May (1976) as a discretization of the logistic equation:

$$p_{n+1} = ap_n(1 - p_n)$$

where a is the growth parameter, n is the discrete time index, and p is a dimensionless population (in May's model, for p outside of the range $0 < p < 1$ solutions will diverge and therefore lose physical meaning). There is no spatial structure in this model. This “classic logistic map” can represent an organism that reproduces in discrete generations with no overlap (e.g., annual plants, some anadromous fish, some benthic invertebrates,

and many insect populations). An array of complicated population dynamics result from this equation, depending on the growth parameter. For $1 < a < 3$ the population reaches steady state after the initial growth period. As a increases, the population experiences a period doubling bifurcation cascade until eventually descending into chaos. Doubling begins for $a \approx 3$ and the onset of chaos begins for $a \approx 3.57$ (May 1976). Beyond the beginning of chaos, the logistic map has pockets of periodicity at special values of $3.57 < a < 4$, e.g., $a = 3.835$ exhibits a period-3 population cycle (Strogatz 1994). The equation has some ecologically impractical constraints, such as population extinction for $a > 4$ and when $p > 1$ (May 1976).

A family of similarly simplistic models exhibit great dynamical complexity (see May and Oster, 1976), and the Ricker model displays qualitatively indistinguishable dynamics to the logistic map (e.g., Andersen 1991). Indeed, the bifurcation diagrams for the two models look incredibly similar. Besides displaying chaotic dynamics over a particular parameter range, these models exhibit other interesting dynamical behaviors, such as long periods of transience (e.g. Hastings & Higgins 1994, Saravia et al. 2000, Labra et al. 2003).

Our model starts with the classic logistic map as one of the simplest models of growth. We employ a normalized Gaussian kernel as the dispersal mechanism, which is a more flexible and ecologically applicable dispersal framework than discretized diffusion (and dispersal kernels have a long and established history of use in the ecological modeling literature, e.g., Chesson and Lee 2005). The dispersal kernel has several advantages, such as decoupling the scale and length of dispersal distance from the

spacing of discrete patches, as well as providing a mechanism to easily change the dispersal distance.

Gaussian kernels are found in seed dispersal models (e.g., Clark et al. 1999), planktonic dispersal models (e.g., Byers and Pringle 2006), and myriad other ecological models. Generally, diffusive-type dispersal effectively models the random dispersal of offspring away from parents. As the number of random movements away from the parent increases, the shape of these random movements forms a Gaussian. This is called the “random walk” model, and is appropriate for small animals such as insects (Skellam 1951). Diffusive-type spread also applies to animals moving over favorable terrain over multiple generations (Krebs 2009, Pielou 1979), or immobile species transported by wind or water (Okubo 1980).

Although diffusive-type dispersal is a useful simplification, there exist many alternative dispersal mechanisms, e.g., non-Gaussian kernels (Kot et al. 1996, Chesson and Lee 2005, Pringle et al. 2009) and asymmetrical advective dispersal (Okubo 1980, Byers & Pringle 2006, Lutscher et al. 2010); these will be included in our future work. However, for this paper, we start with the simplest case and limit ourselves to the symmetrical dispersal-only model. Additionally, we chose to work in a one-dimensional domain, which is an applicable simplification for certain environments, including edge communities bounded by two distinct habitats such as riparian, littoral or coastal areas.

We test ecologically relevant absorbing (dissipative) boundary conditions, and these boundary conditions serve as the basis for the bulk of our ecological analysis. We additionally test periodic boundary conditions to provide deeper insight and as an illustrative comparison with previous literature and with the classic logistic map.

However, these boundaries are not ecologically useful in most real-world systems, as opposite ends of a domain are neither correlated nor connected. Furthermore, periodic boundaries cannot serve as a proxy for an infinite domain. An infinite domain naturally explores the limit of small dispersal (with respect to domain size). Because our dispersal distance expresses length relative to domain size, larger dispersal distances would effectively model the biologically implausible case of infinite dispersal. Boundaries in which 5% of the population survives over the boundary edge and reflecting boundaries were tested to compare with earlier work (because they largely resemble the absorbing and periodic boundary cases, respectively, results are presented in the supplementary material).

With our relatively simple model we partake in a closer examination of the complex dynamics present in a chaotic population while utilizing ecologically reasonable dispersal and boundary conditions. We illustrate how minute changes in dispersal distance, habitat size, or growth rate can dramatically alter the qualitative dynamics of a population (e.g. periodic behavior shifting to chaotic, or vice-versa), and how the boundaries between qualitatively different behaviors may also be complicated. We additionally test a population's response to stochastic elements, simulating the spatial heterogeneity found in real-world populations. Understanding the dramatic and abrupt behavioral changes possible in chaotic populations has significant ecological applications.

Methods:

We explore the logistic map applied to a spatially discrete population along a one-dimensional domain. This is a density-dependent model, where larval production in a discrete patch at time $t+1$ is dependent on the population of that patch at time t . The domain is homogeneous. The number of propagules produced is given by a modified logistic map:

$$l_{i,n+1} = ap_{i,n} \left(1 - \frac{p_{i,n}}{\Delta x}\right)$$

This as the “generalized logistic equation” (Li & Yorke 1975). All variables are dimensionless. Lowercase p and l are dimensionless populations (*sensu* Li & Yorke 1975, Kendall & Fox 1998), a is the growth parameter, and Δx is the fraction of the dimensionless domain occupied by one discrete location (patch), as the sum of Δx across the domain is equal to one. Lowercase n is the time index and i is the space index. Total population of the domain does not depend on the number of patches in the domain, i.e., the carrying capacity of the total population is the same regardless of the number of patches, thus carrying capacity does not depend on Δx . Initial conditions are random. Each patch is assigned a random initial population between zero and 0.001, so that the total population summed across all $N=1001$ patches cannot exceed one (later, we test an additional 1000 random initial conditions to ensure that we are capturing the range of possible dynamics for the system.).

Propagules are then dispersed (convolved) with a normalized Gaussian kernel to obtain the population for a given patch. The normalized Gaussian is:

$$f_i = f(x_i) = \frac{1}{\sigma\sqrt{2\pi}} e^{\frac{-(x_i)^2}{2\sigma^2}}$$

where σ is the standard deviation and x_i is a location in the spatial domain (a patch). We characterize the dispersal distance by the standard deviation of the Gaussian, where the average dispersal distance of a propagule away from a parent is $\sigma\sqrt{2/\pi}$ (the expectation of the half-normal Gaussian). The area under the Gaussian sums to one over infinite space, so Gaussians with large dispersal distances have areas of less than one within the confines of the domain. The discrete convolution of two vectors is given by:

$$p_i = (f * l)_i = \sum_{j=1}^N f_{i-j} l_j$$

where l and f are the two vectors (in our case, the propagule vector and the Gaussian kernel vector), i and j are location indices for the discrete patches, and N is the number of patches in the domain. For absorbing boundaries, the domain is padded on either side, but the portion of the population that is convolved outside of the confines of the domain is considered lost to the system, simulating individuals that disperse out of the habitable range for a species.

We test both periodic and absorbing boundary conditions (as well as reflecting boundaries and absorbing boundaries with 5% survival over the edges in the supplementary material), and iterate 10^4 times (i.e., 10^4 generations). We find that the majority of distributions reach steady state in 10^3 iterations or less, and population distributions for the 10^3 and 10^4 iterations are largely similar in appearance. Although 10^3 or 10^4 iterations to reach steady state indicate significant periods of transience (Hastings & Higgins, 1994), we choose to study the settled system state in order to observe truly persistent chaotic population dynamics. Additionally, the dynamics of a qualitatively settled system are less difficult to describe and interpret.

We test growth parameter a between $3.5 \leq a \leq 4$, overlapping the chaotic parameter space of the classic logistic map. Smaller growth rates of the logistic map exhibit simple dynamics and are well understood. Gaussian standard deviations are tested for the range $1\% \leq \sigma \leq 20\%$ of the domain (average dispersal distances between 0.8% and 16%) in the domain $0 \leq x \leq 1$. The behavior for σ larger than 20% is similar to the behavior at 20%, for reasons described below, so we choose this cutoff to limit our analysis to a smaller parameter space. For large dispersal distances and periodic boundaries, our model essentially reduces to May's model.

To our model, we add a specification that confines the total population to $0 < p < 1$. The original logistic map does not have this constraint, and the population can diverge out of the $0 < p < 1$ bound into negative population numbers. Our model is prevented from producing non-physical outputs by zeroing out discrete locations that produce negative population values. In this way, we are assuming that the population has far exceeded the carrying capacity of that location, and thus has crashed.

The system is nondimensionalized by the domain size, so our model is fully generalized and can be applied to ecological systems of any habitat size/dispersal distance. The domain size is normalized to 1, and because dispersal distance is a proportion of the domain over which a population is spread, one needs only to evaluate the species dispersal distance relative to the total habitat size in order to apply our model to their ecological system of interest.

We test the exponential divergence of neighboring trajectories, a marker of chaos (Lyapunov 1992). Divergence of the trajectories is calculated by allowing two identical populations to evolve identically over time until qualitative behavioral stability is reached

(around 10,000 generations). In this way, we eliminate transients and test for chaotic behavior in the settled state of the system. Next, an arbitrarily small perturbation is applied once over all space to one of the populations. Each discrete location receives a random perturbation drawn from a normal distribution with mean zero and standard deviation 10^{-10} (a number much smaller than the maximum population per patch). The populations continue to evolve over time, but due to the small perturbation to one population, the temporal trajectories are now different. We measure the difference between these two trajectories over 100 generations by taking the L2 norm of the difference over all space (normed sum of differences of each patch to obtain difference in total population). If the divergence of the trajectories is growing over time, the system is considered chaotic and sensitive to arbitrarily small perturbations.

The norm of differences illustrates whether or not the behavior of the total population is chaotic or non-chaotic, i.e., it tells us whether nearby population trajectories diverge, given an arbitrarily small perturbation. Classifying chaos is traditionally accomplished by testing for the divergence of trajectories in each dimension of the system phase space, which in our case has dimension 1001 (testing for trajectory divergence for each patch in the domain). This type of evaluation is described as the Lyapunov spectrum of the system. For each dimension of the phase space, a Lyapunov exponent is calculated, which, when positive, indicates exponential divergence of neighboring trajectories. The collection of 1001 Lyapunov exponents comprise the Lyapunov spectrum. Our calculation provides the same information as a Lyapunov exponent, but in a more succinct way.

In using the divergence of the total population over all space, we could be missing spatial complexities present in the model, and for this reason our future work will investigate the full Lyapunov spectrum of the system in addition to the trajectory divergence over all space. However, populations are presently managed as units. For the ecological purposes of this paper it is both relevant and useful to know the behavioral tendencies of the total population, which we illustrate with the norm of differences.

For non-chaotic distributions, we test the magnitude of the perturbation necessary to create changes in the spatio-temporal behavior of the population. Perturbations are applied to the settled system state, i.e., after 10,000 transients. The perturbation is applied once, across all patches. The patches are each given a random perturbation drawn from a normalized Gaussian with mean of zero and varying standard deviation, to test different magnitudes of perturbation. We test standard deviations in the range of 1% to 50% of carrying capacity.

Results:

Figure 1 illustrates the chaotic parameter space of the classic logistic map for growth rates $a = 3.5$ to $a = 4$, calculated using the norm of differences method above. Red indicates chaotic population behavior while blue indicates non-chaotic behavior.

Results are presented for absorbing boundary conditions unless otherwise stated. Figure 2 provides an example of the four categories of population distribution patterns witnessed. These patterns are referred to as the (a) pattern with kinks (b) frozen random pattern (c) pattern selection regime and (d) supertransient spatio-temporal chaos. The names of the four categories are given by Kaneko (1989) and Willeboordse (2003) but

the sample distribution patterns in figure 2 are from our own model. The pattern with kinks is temporally periodic but does not have a consistent spatial wavelength.

Therefore, population numbers across the domain can have irregular dips or peaks. The frozen random pattern contains pockets of spatiotemporal chaos in an otherwise spatially and temporally periodic distribution. As the population changes over time, most of the domain will have periodic population fluctuations, with small patches experiencing unpredictable population fluctuations. The pattern selection regime is spatially and temporally periodic, and the supertransient spatio-temporal chaos regime has neither a spatially or temporally predictable or detectable pattern.

Figure 3 provides a snapshot of population dynamics for the full range of parameters tested with random initial conditions. Absorbing boundary conditions are presented in figure 3a, periodic boundary conditions in figure 3b. The red color indicates that the given population distribution experiences exponential divergence of neighboring trajectories when subjected to a perturbation (i.e. chaotic). Periodic population distributions are often observed within the chaotic parameter space of the classic logistic map, with almost complete elimination of chaos for the largest dispersal distances of the absorbing boundary conditions. Different initial conditions can evolve into different basins of attraction (e.g., Schneider et al. 2007), so the behavior observed for each parameter combination in figure 3 is an example of the possible population dynamics for that given parameter combination, as a different set of random initial conditions can yield different spatial and temporal behavioral outcomes. Figure 3 is equivalent to the information presented in a bifurcation diagram (e.g., May 1976), but allows us to easily

display the spatiotemporal population dynamics of the full range of parameter combinations tested.

To gauge typical versus atypical population behavior for each parameter combination, we run the model 1000 times with 1000 random initial conditions for each parameter combination and iterate for 10^4 generations, as before. We calculate the norm of trajectory divergence for each model run and results are presented in figure 4. The color and size of the circles corresponds to the number of model runs with chaotic behavior out of 1000 total runs. Many parameter combinations have consistent behavioral patterns, where nearly all of the 1000 random initial conditions have consistently chaotic or consistently non-chaotic behavior. Small dispersal distances are less behaviorally consistent, e.g., with some parameter combinations yielding half chaotic and half non-chaotic behaviors.

Moving horizontally across a row in figure 3a, we see that a frozen random pattern is often observed between two pattern selection regimes of differing wavelength. The wavelength is dependent on the growth parameter and dispersal distance/habitat size, where wavelength decreases with increasing a or decreasing dispersal distance/increasing habitat size. The analogous phenomenon found for coupled patch models is wavelength scaling linearly with coupling distance (Willeboordse 2003). We investigate the relationship between the frozen random pattern and the pattern selection regimes by selecting an example growth rate and examining dispersal distances between the ranges of 0.8% to 16% of domain size ($1\% \leq \sigma \leq 20\%$) as before, but in smaller increments. A very clear pattern emerges, where frozen random patterns with varying levels of spatial

chaos exist between two pattern selection regimes of different wavelengths. A movie of this phenomenon is available in the supplementary material (Online Resource movie 1S).

We also illustrate this phenomenon in figure 5, where regions of chaos appear between regions of non-chaotic behavior. The non-dimensional spatial extent of both chaotic and non-chaotic sections becomes longer as the wavelength increases with increasing dispersal distance, or equivalently, with decreasing domain size. Smaller dispersal distances experience more frequent behavioral switching due to the frequent transitioning between wavelengths that fit spatially in the domain versus wavelengths that do not (an integer number of waves in the domain versus a non-integer number of waves). This is likely due to the fact that as wavelength becomes smaller, the difference between integer wavelengths that fit in the domain is also smaller: i.e., the difference between $\lambda=1/9$ and $\lambda=1/10$ is smaller than the difference between $\lambda=1/2$ and $\lambda=1/3$. The larger wavelengths can maintain spatially periodic (or nearly periodic) behavior through incremental changes in dispersal distance and thus retain the same behavior for larger parameter windows (they also have longer stretches of non-periodic behavior). This is exhibited by the longer stretches of blue or red color with increasing dispersal distance in figure 5.

Because of the frequent behavioral switching for smaller dispersal distances, chaotic behavior is more difficult to avoid. Non-chaotic parameter windows become shorter and therefore a randomly selected parameter in a non-chaotic window is closer to the chaotic parameter windows on either side. A small change in the dispersal distance/domain size could easily result in a switch from periodic to chaotic behavior.

No real-world system is free of external perturbations, so to apply our model to real ecological systems, we must investigate perturbation. Our norm of differences analysis reveals which parameter combinations are sensitive to slight perturbation, but we now investigate the magnitude of perturbation necessary to change the population pattern dynamics (e.g., from a pattern selection regime to a frozen random pattern). We apply perturbations to populations representing three behavioral regimes: pattern with kinks, frozen random pattern, and pattern selection regime. For each behavioral regime, several growth + dispersal distance parameter combinations are selected. Perturbations between 1% to 50% of carrying capacity are applied.

In the pattern selection regimes we witness a slow increase in aperiodic behavior between perturbations of 1% to 10% of carrying capacity. The pattern selection regimes begin to resemble frozen random patterns, where the structure of the previously periodic behavior is still obvious, but the spatial distributions over multiple time iterations do not stack perfectly over each other (i.e., the population distribution is non-repeating). Near the 10% perturbation, the population distributions resemble chaotic distributions. Increasing the perturbations from 10% to 50%, the populations generally remain in this regime, though for certain combinations of growth + dispersal distance + perturbation magnitude we witness a recurrence of nearly periodic behavior, suggesting that the random perturbation, effectively changing the growth rate, pushed the population near a stable periodic orbit. A similar progression is witnessed for the frozen random patterns, with a slow increase in chaotic behavior between 1% and 10% and a transition to fully resembling spatiotemporal chaos between 10% and 20%. Figure 6 provides an example. Frozen random patterns can also have random occurrences of nearly periodic behavior at

larger perturbations, and in some instances, the perturbation pushes the dynamics onto a more well-behaved attractor than the perturbation-free system. Spatiotemporally chaotic population distributions remain that way throughout the various tested perturbation levels.

If the perturbation is applied only once, the majority of population distributions re-settle in their original distribution patterns. For patterns that would otherwise be stable, consistent perturbation is required to keep the population unstable. The unique exception appears to be for behavioral regimes that were pushed onto a more well-behaved attractor than the original perturbation-free system. The periodic (or nearly periodic) behavior endures long after the perturbation was applied, shifting e.g., frozen random patterns into pattern selection regimes.

To aid in interpretation of our absorbing boundaries output, we compare the absorbing boundaries case with periodic boundaries, a more well-studied, but less ecologically relevant system (figure 3a versus figure 3b). An important distinction between these boundary conditions is the pronounced suppression of growth due to edge mortality for absorbing boundaries. For example, with absorbing boundaries, a dispersal distance of 0.16 and a of 3.8 with an initial population of 0.01, iterated once, grows to 0.0354 (in the absence of density dependence) due to a portion of the population settling outside of the habitat domain. An a of 3.8 has been reduced to an actual growth rate of 3.54. While a growth rate of 3.8 is well within the bounds of chaotic behavior for the classic logistic map, it has been effectively reduced to 3.54, below the threshold for chaos. In the periodic boundaries case, this suppressed growth is absent, as the only limiting factor for growth in the periodic boundaries case is density dependence.

For the largest dispersal distances, the periodic boundaries cases succeed at homogenizing the domain due to the population wrapping around the edges. The population distribution is completely uniform across the domain, appearing as a straight line (figure 3b). Because the population is uniform across the domain, it can be treated as a point-source population and the model has essentially collapsed back into the parameter space of the classic logistic map. The largest dispersal distances of the absorbing boundaries case fail to accomplish this complete homogenization due to increasing mortality over the boundary edge with increasing dispersal distance. Instead, the population distributions appear as bell-shaped curves in figure 3a. The absorbing boundaries subsequently do not recover towards the parameter space of the classic logistic map with increasing dispersal distance, and we witness an obvious reduction in chaotic behavior with increasing dispersal, due in part to dispersal-driven mortality.

Discussion and Conclusion:

1. Model dynamics

With our simple model, we witness a variety of behaviors, dependent on the growth rate and dispersal distance/domain size. This system illustrates how well-behaved periodic population dynamics can actually be driven by equations which retain the potential for chaotic dynamics, given a different parameter set or an external perturbation. Change in growth rate, dispersal distance, or domain size could shift the population into a different behavioral regime. Such dramatic change in behavior would be unexpected and

misinterpreted if the presence of nonlinear dynamics was not considered. As illustrated in figure 5, frequent switching of qualitative behavior occurs with small changes in parameters, particularly for small dispersal distances (with respect to domain size). Boundaries between chaotic/non-chaotic behavior start to appear fractal in nature; the same pattern appears at finer and finer spatial scales. In a real-world setting, this could translate to nearly constantly evolving behavioral patterns for a population experiencing flux in dispersal distance, habitat size, or growth rate. Such behavior could be interpreted as stochastic without relevant insight into the system dynamics.

Frequent changes in growth, dispersal, or domain size are easy to imagine in a real-world ecological system, as many environmental factors affect these parameters. For example, ocean acidification and coral bleaching leads to fragmented coral reef habitats, changing the domain size over which coral reef fish can successfully disperse and survive (Munday et al. 2009). Although the effects of habitat fragmentation do not depend only on the altered dispersal distance and/or domain size of a species, our model could help predict changes in qualitative behavior based on changes in these two factors. For this ecological system, our model would predict a possible change in behavior due to the altered ratio of dispersal distance versus domain size, along with increased edge mortality of the dispersing adolescent larval fish. Nearly any species influenced by changing habitat could be subject to profound changes in population dynamics if said population is nonlinear or chaotic. Understanding that the population changes aren't stochastic, and understanding the mechanisms driving the changes is important for future preservation and management of the population.

Our model yields periodic and quasi-periodic behavior through the full chaotic growth range of the classic logistic map. The appearance of non-chaotic behavior can be attributed to several factors. For absorbing boundaries, we witness a suppressed growth rate due to edge mortality, which, especially for large dispersal distances, can push the realized growth rate below the chaotic threshold. For parameter combinations where edge mortality is not the defining influence, and for periodic boundaries, we witness periodic behavior when the dispersal distance matches with an integer number of wavelengths in the domain. These periodic patterns appear as a “cancellation” of the inhomogeneity of the chaotic signal with the homogenizing dispersal (Kaneko 1989a). Between these wavelengths exists a transitional quasi-periodic spatial pattern, where a nearly integer number of waves in the domain is counteracting the chaotic dynamics (but the chaos is not canceled entirely). Additionally, there exist special a values in the parameter space of the classic logistic map that yield periodic behavior (figure 1). As we test myriad dispersal distance and growth rate combinations, some of those combinations could result in growth rates equal to those special a values.

2. Stochasticity

Although our growth and dispersal model has no intrinsic stochasticity, we add external stochastic perturbations, as real-world populations are certainly subject to them. In this way we test the stability of the model when subjected to large perturbations that may occur in nature. The model displays extreme sensitivity to change in parameters, but is more robust to perturbations of the population. Populations do experience short-term change in dynamics for perturbations $\approx 10\%$ of carrying capacity or larger (figure 6), but

the perturbations need to be applied continuously in order to hold the population in the new behavioral regime. The population distributions had a tendency to settle back to their pre-perturbation dynamics without repeated disturbance, which in real-world populations would indicate resilience to one-time perturbations. One exception to this trend is when the stochastic perturbation moves the population onto a stable periodic orbit, where it remains thereafter. This illustrates how stochastic perturbation is not necessarily always a vehicle for destabilization in a chaotic system.

To affect change in population dynamics, stochastic perturbations need to be sustained over time. Some populations may certainly be subjected to large, continuous perturbations, and those populations would have a much smaller parameter space of stable population dynamics than populations that are only subjected to low-level perturbations. Our results have shown that all populations, regardless of perturbation, are highly sensitive to changes in fundamental population features, e.g., domain size, and these changes are more important to the long-term dynamics of the population than temporary stochastic elements affecting population numbers, e.g., disease. A large stochastic perturbation may temporarily induce chaotic behavior in an otherwise well-behaved population, but if a fundamental feature of the population is altered, e.g., due to human habitat development, this could lead to profound and permanent changes in the population dynamics.

3. Basins of Attraction

Our exploration of basins of attraction indicates that some parameter combinations have multiple basins, particularly at smaller dispersal distances (figure 4).

Small variations in initial conditions can lead the population to chaotic or non-chaotic long-term behavior. Multiple basins for the same parameter set are common in the chaotic literature, e.g., Schneider et al (2007). The geometry dividing the basins can be very complex (Chantry & Schneider, 2014), and this will be explored in our future work. Before the dynamics settle into a basin, there is a period of chaotic transience. Transients for our model (and similar past models) can be very long, thus the behavior of the transient period can be ecologically relevant (Hastings and Higgins 1994). An interesting outcome of models like these is the apparent regime shift of the population dynamics without any external forcings (where we use regime shift as defined by Norberg and Cumming 2008). Examination of regime shifts as internally-driven outcomes of chaotic populations is an interesting avenue of exploration (while acknowledging that, for many populations, regime shifts are due to external forcings).

Conclusion

Classic models from the 1970s through 1990s introduced chaotic theory into the ecological literature. The applications for these models were largely theoretical, given the simplicity of the models and the computational limitations of the time. Here, we revisit these classic models with modern numerical techniques to examine the systems more closely and to add elements of ecological realism such that the models can be employed for concrete ecological applications. Combining improved knowledge of chaos with improved knowledge of ecology, we hope to see an increasing number of applications of chaotic theory to real-world systems.

Integrating easily interpretable chaotic models into the ecological literature is crucial as chaotic behavior becomes more directly detectable in a wide range of ecological systems. As we have demonstrated, simple chaotic models can exhibit a variety of complex behaviors that are often very sensitive to small changes in the system. The ecological implications are numerous, and we have presented only a small selection.

We envision our model being utilized in several ways. If chaotic dynamics have been detected in a system (using one of the methods cited in the introduction), the model could help predict future dynamics and the likelihood of a change in dynamics due to changes in one of the fundamental system parameters. If a species is undergoing some profound modification, e.g., habitat destruction, and its population dynamics subsequently change in an unpredictable way, our model could help demystify these changes and evaluate the likelihood of recovering the previous population dynamics. Because it is a discrete-time, diffusive-type dispersal model, it can be applicable to insects, microorganisms, seed dispersal, and species in aquatic environments that lack a dominant current. Because it is nondimensionalized, it can be applied to populations of any size over any size domain. Our future work will expand the model to advective environments appropriate for many marine fish species, which have been shown to display chaotic dynamics (Glaser et al. 2014).

Understanding chaotic behavior in terms of ecological systems is especially important in light of our rapidly changing environment. Changes in factors such as habitat size, resource availability, or temperature can abruptly and dramatically alter population behaviors if these factors also drive variables of a system with the potential for chaotic dynamics. Anticipating and understanding dramatic population changes will

be crucial as we seek to preserve and manage vulnerable populations. Concepts from chaos, illustrated through ecologically applicable models, can be helpful in this endeavor.

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Figure Captions

Fig. 1 Chaotic (red) versus nonchaotic (blue) parameter space of the classic logistic map across growth rates $a = 3.5$ to $a = 4$

Fig. 2 Examples of population distribution patterns: pattern with kinks (a), frozen random pattern (b), pattern selection (c), and supertransient spatio-temporal chaos (d). The growth parameter a increases in each image ($a = 3.5, 3.7, 3.8, 4$). Dispersal distances are 0.008, 0.016, 0.024, 0.008 (in a domain of size 1). Example graphs are taken from absorbing boundaries conditions. Patterns are created by overlapping the last 100 population distributions of 10^4 total iterations.

Fig. 3a & 3b Population distribution patterns for dispersal distances of 0.008 to 0.160 ($0.01 \leq \sigma \leq 0.2$) and growth parameters $3.5 \leq a \leq 4.0$. Figure 3a displays absorbing boundary results, figure 3b displays periodic boundary results. Within each subplot, the x-axis is the domain and the y-axis is the corresponding population at that discrete location in the domain. The observed patterns are created by overlapping the last 100 population distributions of 10^4 total iterations. Red graphs indicate parameter combinations that yield chaotic dynamics.

Fig. 4 Exploration of the range of dynamical possibilities for each parameter combination, absorbing boundaries. Each combination was tested 1000 times with 1000 random initial conditions. The color and size of the circles in the graph correspond to how many of the population distributions were chaotic, out of 1000, using our norm of differences classification system. As before, we test for chaotic behavior by applying an arbitrarily small perturbation to the settled system, i.e., after 10,000 iterations.

Fig. 5 Examining behavior at dispersal distances from 0.008 to 0.16 ($0.01 \leq \sigma \leq 0.2$), increments of 0.0005, $a = 3.85$. Red indicates chaotic behavior, blue indicates non-chaotic behavior. In the top graph we explore the full range of dispersal distances, while the bottom graph examines the behavior between dispersal distances of 0.008 to 0.028, at increments of 0.00005.

Fig. 6 Population distributions for growth rate = 3.90, dispersal distance 0.04, with increasingly larger perturbations moving along the x-axis. Graphs are 100 overlapped population distributions immediately following the perturbation.

Figure 1

Figure 2

Figure 3A

Figure 3B

Figure 4

Figure 5

Figure 6