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Reactivity, Attenuation, and Transients in Metapopulations[*]

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Abstract. Transient dynamics often differ drastically from the asymptotic dynamics of systems. In this paper we analyze transient dynamics in birth-jump metapopulations where dispersal occurs immediately after birth (e.g., via larval dispersal). We address the choice of appropriate norms as well as the effect of stage structure on transient dynamics. We advocate the use of the ℓ_1 norm, because of its biological interpretation, and extend the transient metrics of reactivity and attenuation to birth-jump metapopulations in this norm. By way of examples we compare this norm to the more commonly used ℓ_2 norm. Our focus is the case where transient dynamics are very different than asymptotic dynamics. We provide simple examples of metapopulations where this is the case and also show how increasing the number of habitat patches can increase this difference. We then connect the reactivity and attenuation of metapopulations to the source-sink classification of habitat patches and demonstrate how to meaningfully measure reactivity when metapopulations are stage-structured, with a focus on marine metapopulations. Our paper makes three primary contributions. First, it provides guidance to readers as to the appropriate norm and scalings for studying transients in birth-jump metapopulations. Second, it provides three examples of transient behavior in metapopulations involving slow-fast systems, crawl-bys, and high dimensionality. Third, it connects the concepts of reactivity and attenuation to the source-sink classification of habitat patches more commonly found in marine metapopulations.

Key words. transient dynamics, metapopulation, reactivity, source-sink dynamics, marine systems

AMS subject classifications. 92D25, 92D40, 34A30, 34C11

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1. Introduction.

Transient dynamics, those that occur over short timescales, can often be vastly different from the asymptotic or long-term dynamics of ecological systems. However, throughout the history of mathematical biology much of the work has focused on determining the asymptotic dynamics of biological systems. While the study of long-term dynamics has given ecologists many tools to analyze the behavior of populations, these tools are often not the same as those required to understand transient dynamics. Recently Hastings et al. [21] have shown that transient dynamics are much more ubiquitous than previously assumed and

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long transients occur in many different ecological systems, from plankton and coral to voles and grouse. Studying the transient dynamics of an ecological system can give useful insight into the different processes that may occur after a disturbance, change in environmental conditions, or change in human intervention to a system. In some marine systems that are driven by environmental fluctuations, such as the Dungeness crab, transient dynamics may in fact be key to understanding how these systems behave [23].

There has also been a recent push to characterize the different types of systems that display long transient dynamics that differ significantly from their asymptotic dynamics [36, 21, 20, 19]. Hastings et al. [21] have loosely categorized four different drivers of long transient dynamics in ecological systems: ghost attractors and crawl-bys, slow-fast dynamics, high dimensionality, and stochastic noise. These categories are not always distinct and certain systems may indeed fall into multiple categories. For example, a predator prey system may have a crawl-by past a saddle that drives the transient dynamics in this system, but this could also be thought of as a difference in timescales of the predators decline due to lack of prey. For metapopulations the main driver of transient dynamics is often the high dimensionality arising due to spatial structure, though these transient dynamics may be exacerbated by the other drivers as well.

Some of the earliest studies of systems that could generate long transients were systems with spatial structure [22, 31]. It seems intuitive that spatial structure or spatial heterogeneity can drive some sort of transient dynamics in a system. If individuals start in one location in a habitat, especially a poor habitat, then it will take time before they can spread over the entire habitat and the long-term population dynamics begin to emerge. What is surprising is that spatial structure can also give rise to so called long-lived transients, where the transient dynamics are extensive enough that they continue on timescales past which we typically measure biological populations [22].

One method of adding spatial structure to a population is to formulate it as a metapopulation, where distinct populations live on habitat patches that are connected via dispersal or migration. Metapopulation models were originally proposed by Levins [30] to model patch occupancy in habitats consisting of isolated habitat patches, but these early models used space implicitly rather than explicitly. Later metapopulation models have included space explicitly by allowing for differing habitat quality on patches or differing dispersal between patches [17, 16], though often these models are focused on the proportion of occupied patches rather than the population size on each patch. However, many marine metapopulation models as well as epidemiological metapopulation models explicitly track the number of individuals on each patch as well as movement or dispersal between patches [31, 2, 14, 3]. In this paper we model the metapopulation structure following this spatially explicit framework where individuals are tracked rather than the proportion of occupied patches.

Another benefit of the metapopulation framework is that habitat patches can be classified into source patches and sink patches. This classification can occur in many different ways [14, 43, 29], but commonly a source is a productive habitat patch and a sink is a poor habitat patch. Early measures of sources and sinks were mainly focused on connectivity between patches, but more recently it has been understood that it is the interplay between patch connectivity and local patch productivity that characterizes patches as sources or sinks, especially in marine metapopulations. One of the new and easily tractable metrics that embodies this relationship comes from the theory of next-generation matrices and the basic reproduction number, R_0. This framework, originally developed in epidemiology, has been used to characterize sources and sinks in populations of mussels, salmon, and sea lice on salmon farms [29, 26, 18].

While metapopulation theory has previously been used to classify patches as sources and sinks, other metrics have been used to characterize the transient dynamics of systems. Reactivity was initially introduced by Neubert and Caswell [39] to measure the maximum initial growth rate of a system over all possible perturbations from an equilibrium. If the maximum initial growth rate is positive, then the system is reactive. Complementing reactivity is the amplification envelope, which is a measure of how large solutions can grow over time after initial perturbations. Later, Townley and Hodgson [53] introduced attenuation as the opposite metric to measure initial decline of populations; a system attenuates if the minimum possible growth rate declines following a perturbation. Reactivity and attenuation are then most interesting when they are different from the stability of the equilibrium of a system—when a system attenuates but is unstable, or is reactive but stable—and it is on these situations that we focus this paper. Biologically these are populations that begin by declining but eventually increase, or begin by increasing but eventually decline.

It should be noted that reactivity, attenuation, and the amplification envelope are all defined from the linearization of a nonlinear system about an equilibrium. These measures are therefore most useful around hyperbolic equilibria, where the dynamics of the nonlinear system can be well approximated by the dynamics of the linear system. If an equilibrium is not hyperbolic, then the trajectories in the nonlinear system may no longer be similar to the linearization by which reactivity, attenuation, and the amplification envelope are defined. Even around a hyperbolic equilibrium the trajectories of the nonlinear and linearized systems may diverge as they move away from the equilibrium. Here we use the technique of linearization to determine reactivity and attenuation as others have before us, but want to emphasize these caveats as they are often brushed over in the transient literature.

In this paper we apply these transient measures of growth to a class of biological metapopulation models where there is no migration between population patches, only birth on new patches. These are a subset of birth-jump processes [24] and include models for marine meroplanktonic species, where larvae can travel through the ocean between population patches but adults remain confined to a habitat patch. Specific species that exhibit this structure include sea lice [1], corals and coral reef fish [10, 28], barnacles [44], Dungeness crabs [6], sea urchins [6], and many other benthic marine species [11]. This type of system also encompasses many plant species where seeds are carried between suitable habitat patches [27], and depending on the census timing could also include insect species where there is one large dispersal event between habitat patches, such as the spruce budworm [32, 37, 57] and mountain pine beetle [45]. Last this class of models also includes multipatch or multicity epidemiological metapopulation models where infections can spread between patches, for example, infected residents of a city may travel and infect residents of other cities before returning home [2]. We focus on the transient dynamics that can occur around the extinction state of these systems.

The aims of this paper are threefold. The first is of a technical nature: if we want to study reactivity and attenuation, what norm should we use and how do we calculate these quantities from the dynamical system? In section 2 we demonstrate how to calculate reactivity and attenuation using the biologically intuitive ℓ_1 norm in birth-jump metapopulations, and in section 6 we show how to add a weighting to this norm to calculate reactivity and attenuation if the metapopulation is stage-structured. The second aim of this paper is pedagogical, to provide simple examples of metapopulations that exhibit interesting transient behavior that is different from their asymptotic behavior as well as transient behavior that is different depending on the norm. In section 2 we provide examples that illuminate the difference between reactivity and attenuation in the ℓ_1 and ℓ_2 norms, in section 3 we provide examples that illustrate the potential difference between the transient and asymptotic dynamics of metapopulations, and in section 4 we provide an example of how increasing the number of habitat patches can accentuate this difference. The last aim of this paper, and the focus of section 5, is to connect reactivity and attenuation to the source-sink classification of habitat patches, of which there exists a large body of literature in marine metapopulations, thus relating these instantaneous and generational transient measures of growth and decay.

Chronologically the paper is structured as follows. In section 2 we use the ℓ_1 norm as a biologically intuitive measure of reactivity and attenuation in birth-jump metapopulations and provide examples to demonstrate how measurement in this norm differs from the commonly used ℓ_2 norm. In section 3 we use simple two-patch metapopulation examples to demonstrate that the transient dynamics of these systems can be vastly different from their asymptotic dynamics, and in section 4 we provide an example of how increasing the number of habitat patches in a metapopulation can enhance this difference. In section 5 we show how to connect the reactivity and attenuation of a metapopulation to the source-sink classification of habitat patches, and in section 6 we show how to appropriately measure the reactivity and attenuation of a metapopulation when the population is stage structured using a weighted ℓ_1 norm.

2. Extending the general theory of transients to metapopulations.

In this section we apply the metrics of reactivity [39] and attenuation [53] to the zero equilibrium of general systems of single-species metapopulations and thus focus on the transient dynamics that can occur around the extinction state of these systems. In order to present our work in a general form, we model the dynamics of a metapopulation of a single species on n patches around the zero equilibrium with the system:

$$x'(t) = Ax(t), \qquad x(0) = x_0, \tag{2.1}$$

where $A = [a_{ij}]$ is a real irreducible Metzler matrix ($a_{ij} \geq 0$ for all $i \neq j$) of order n, $x(t)$ is a population vector containing the population of the species on each patch, and the initial condition x_0 is a small perturbation of the zero equilibrium. This most often represents the linearization of a nonlinear system, which more completely captures the dynamics of the population, but could also represent the full dynamics of a linear system if density dependence was not important to the population dynamics.

For the analyses in this paper we focus on biologically realistic single-species metapopulations where the entries of $x(t)$ are nonnegative when beginning with a nonnegative initial perturbation, x_0. This condition is equivalent to requiring that A be an essentially nonnegative (Metzler) matrix, such that all the off-diagonal entries of A are nonnegative (Theorem 2.4 in [51]). Biologically this means that the presence of individuals on one patch cannot contribute to the decline of a population on another patch and that the population on each patch will not become negative.

2.1. Reactivity and attenuation using the ℓ_1 norm. To analyze the transient dynamics of this metapopulation we begin by introducing some definitions from Neubert and Caswell [39]. An equilibrium is *reactive* if there is an initial perturbation x_0 such that the initial growth rate of the total population is positive. The mathematical definition of reactivity from Neubert and Caswell [39], using notation from Lutscher and Wang [33], is

$$\bar{\sigma}_\omega = \max_{||x_0||_\omega \neq 0} \left[\frac{1}{||x(t)||_\omega} \frac{d||x(t)||_\omega}{dt} \bigg|_{t=0} \right], \tag{2.2}$$

where $x(t)$ is a solution to (2.1) and ω specifies the norm to be used to calculate reactivity; if the ℓ_1 norm is used, then $\omega = 1$, and if the ℓ_2 norm is used, then $\omega = 2$. If $\bar{\sigma}_\omega > 0$, then the equilibrium is reactive, and if $\bar{\sigma}_\omega \leq 0$, then the equilibrium is not reactive. Neubert and Caswell [39] use the ℓ_2 norm to measure the population size and show that $\bar{\sigma}_2$ is the maximum eigenvalue of $(A + A^T)/2$. However, the ℓ_2 norm lacks a reasonable biological interpretation, and so others have instead used the ℓ_1 norm to define reactivity [26, 52, 48]. Biologically, the ℓ_1 norm,

$$||x||_1 = \sum_{i=1}^{n} |x_i|, \tag{2.3}$$

can be interpreted as the total population on all patches of a metapopulation whereas the ℓ_2 norm,

$$||x||_2 = \sqrt{\sum_{i=1}^{n} x_i^2}, \tag{2.4}$$

is the Euclidean distance of the total population away from the origin. We show in this work that the ℓ_1 norm is convenient to determine reactivity from the population matrix A in single species metapopulations.

In contrast, an equilibrium *attenuates* if there is an initial perturbation x_0 for which the initial growth rate of the total population declines [53]. This is formally defined as

$$\underline{\sigma}_\omega = \min_{||x_0||_\omega \neq 0} \left[\frac{1}{||x(t)||_\omega} \frac{d||x(t)||_\omega}{dt} \bigg|_{t=0} \right]. \tag{2.5}$$

If $\underline{\sigma}_\omega < 0$, then the equilibrium attenuates, and if $\underline{\sigma}_\omega \geq 0$, then the equilibrium does not attenuate.

Comparing the definitions of attenuation and reactivity we can see that it is possible for an equilibrium to be both reactive and to attenuate if there are certain initial perturbations for which $\bar{\sigma}_\omega > 0$ is achieved and others such that $\underline{\sigma}_\omega < 0$. In relation to the stability of an equilibrium, all stable equilibria attenuate and all unstable equilibria are reactive (Theorem 2.3). Reactivity and attenuation are then most interesting when they are different from the stability of the equilibrium: when an equilibrium is reactive but stable, so that the total population initially grows but eventually declines, or when an equilibrium attenuates but is unstable, so that the total population declines but eventually grows. It should also be noted that the only systems that are not reactive and do not attenuate are those in which the total population size remains constant for all times. In this paper we sometimes refer to the reactivity and attenuation of a system, rather than an equilibrium, and in this case we are referring to the reactivity and attenuation of the zero equilibrium, around which we have linearized a system.

The last measures that we define here to use in some later sections are the *amplification envelope* and the *maximum amplification*. The amplification envelope is the maximum possible deviation of a solution away from the steady state at time t after any initial perturbation x_0, which Neubert and Caswell [39] define mathematically as

$$\rho(t) = \max_{||x_0||\neq 0} \frac{||x(t)||}{||x_0||}. \tag{2.6}$$

The maximum amplification is simply the maximum of the amplification envelope over all times:

$$\rho_{\max} = \max_{t\geq 0} \rho(t) = \max_{\substack{t\geq 0\\ ||x_0||\neq 0}} \frac{||x(t)||}{||x_0||}. \tag{2.7}$$

We do not use ω to differentiate between norms here as we only use the amplification envelope and maximum amplification with the ℓ_1 norm in subsection 3.1 and section 4. The amplification envelope need not be achieved by a single perturbation that produces a maximal solution for all times; rather different perturbations may produce the maximal deviation for different times. While reactivity and attenuation quantify the short time response to a perturbation, the amplification envelope and maximum amplification quantify how large a perturbation can become and how long growth can last. It is for these purposes that we use the amplification envelope and maximum amplification in subsection 3.1 and section 4.

Now before quantifying the reactivity and attenuation of the entire metapopulation, let us first determine the initial growth rate of the population if we begin with one individual on patch j. We call this initial growth rate λ_j, and mathematically we define

$$\lambda_j = \sum_{i=1}^{n} x_i'(0)$$

with $x_0 = e_j$, where e_j is the vector of length n with 1 in the jth entry and 0s elsewhere. In terms of system (2.1) this simplifies to the jth column sum of A,

$$\lambda_j = \sum_{i=1}^{n} a_{ij}.$$

The initial growth rate for a given patch j, λ_j, can also be calculated from the lifecycle digraph as the sum of all the outgoing birth rates from a patch minus the death rate on that patch, where any paths describing movement of individuals between patches are ignored. See Figures 3, 5, 7, and 8 for examples of lifecyle graphs and Caswell [8] for further reference. We can then connect this patch specific initial growth rate with the total growth rate, or reactivity, using the following lemma.

Lemma 2.1. *Reactivity under the ℓ_1 norm in (2.2) is equal to the maximum column sum of A in system (2.1),*

$$\bar{\sigma}_1 = \max_{1\leq j\leq n} \lambda_j = \max_{1\leq j\leq n} \sum_i a_{ij}.$$

Proof. Since $x_j \geq 0$ for all j, the absolute value signs in (2.2) can be dropped and so

$$\begin{aligned}\bar{\sigma}_1 &= \max_{||x_0||_1=1} \left[\frac{d||x||_1}{dt}\bigg|_{t=0} \right] = \max_{||x_0||_1=1} \left[\frac{d}{dt}\sum_{i=1}^{n} x_i \bigg|_{t=0} \right] \\ &= \max_{||x_0||_1=1} \left[\sum_{i=1}^{n} \frac{d}{dt} x_i \bigg|_{t=0} \right] = \max_{||x_0||_1=1} \left[1^T x' \bigg|_{t=0} \right],\end{aligned}$$

where 1^T is a row vector where every entry is equal to 1. Substituting $x' = Ax$ from system (2.1) gives

$$\bar{\sigma}_1 = \max_{||x_0||_1=1} \left[1^T A x_0\right] = \max_{||x_0||_1=1} \left[\sum_{j=1}^{n} \left(\sum_{i=1}^{n} a_{ij} \right) x_{0j} \right].$$

Now let k be such that $\sum_{i=1}^n a_{ik} = \max_{1\leq j\leq n} \sum_{i=1}^n a_{ij}$. Then, with $||x_0||_1 = 1$,

$$\sum_{j=1}^{n} \left(\sum_{i=1}^{n} a_{ij} \right) x_{0j} \leq \left(\sum_{i=1}^{n} a_{ik} \right) \sum_{j=1}^{n} x_{0j} = \left(\sum_{i=1}^{n} a_{ik} \right)$$

with equality when $x_{0j} = \begin{cases} 1, & j = k, \\ 0, & j \neq k. \end{cases}$ Therefore,

$$\bar{\sigma}_1 = \max_{1\leq j\leq n} \left(\sum_{i=1}^{n} a_{ij} \right) = \max_{1\leq j\leq n} \lambda_j.$$

■

With a similar proof we can connect the patch specific initial growth rate to attenuation via the following lemma.

Lemma 2.2. *Attenuation under the ℓ_1 norm in (2.5) is equal to the minimum column sum of A in system (2.1),*

$$\underline{\sigma}_1 = \min_{1\leq j\leq n} \lambda_j = \min_{1\leq j\leq n} \sum_i a_{ij}.$$

It should be noted, as can be seen in the proof of Lemma 2.1, that the maximum possible growth rate occurs if the initial population is all on the patch with the maximum λ_j, and the minimum possible growth rate occurs if the initial population is all on the patch with the minimum λ_j.

2.2. Comparing reactivity in the ℓ_1 and ℓ_2 norms. Here we present some examples of systems that are reactive in ℓ_1 but not in ℓ_2 and vice versa to illuminate the difference between measuring reactivity in the two norms. It has previously been noted that reactivity depends on the norm and scaling [39, 33] and the following examples help clarify the underlying biological and mathematical meaning of the two norms.

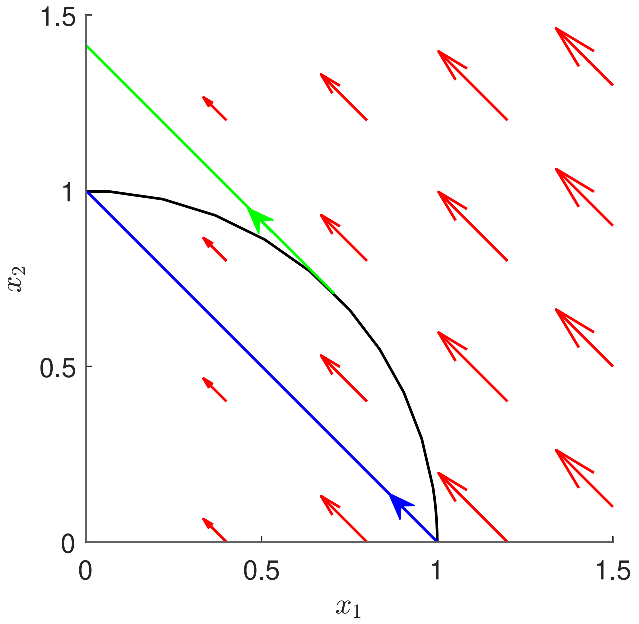


Figure 1. *The phase plane for system* (2.1) *with* $A = \left[\begin{smallmatrix} -1 & 0 \\ 1 & 0 \end{smallmatrix}\right]$*, which is reactive in* ℓ_2 *but not in* ℓ_1*. The line* $x_1 + x_2 = 1$ *and the circle* $x_1^2 + x_2^2 = 1$ *geometrically depict* $||x|| = 1$ *in the* ℓ_1 *and* ℓ_2 *norms, respectively. The derivative vectors for the phase plane are shown in red and two different initial trajectories are shown in green and blue. The green trajectory is an example that is reactive in* ℓ_2 *but not in* ℓ_1*, and the blue trajectory is another example that is not reactive in* ℓ_1*.*

Example 1. First, we present an example that is reactive in ℓ_2 but not in ℓ_1. Reactivity in ℓ_2, $\bar{\sigma}_2$ can be calculated as the maximum eigenvalue of $(A + A^T)/2$ [39]. Take system (2.1) with

$$A = \begin{bmatrix} -1 & 0 \\ 1 & 0 \end{bmatrix}.$$

This system simply redistributes individuals from patch 1 to patch 2, and the phase plane is shown in Figure 1. It is not reactive in the ℓ_1 norm ($\bar{\sigma}_1 \leq 0$) because the total population size is not increasing, but it is reactive in ℓ_2 ($\bar{\sigma}_2 > 0$). This highlights how measuring reactivity in the ℓ_2 norm can at times defy our biological expectation of what reactivity should mean—the growth of a population—and reinforces our rationale for using the ℓ_1 norm to measure reactivity in metapopulations. While the matrix A is reducible and this system is only semistable, and thus may be considered a borderline example, if a_{22} is replaced by a small negative number, $-\epsilon$, and a_{12} is replaced by a small positive number, $\epsilon/2$, then for sufficiently small ϵ, A will be irreducible and the system will now be stable, but will still be reactive in ℓ_2 and not in ℓ_1.

Example 2. The second example, which is reactive in ℓ_1 but not in ℓ_2, is system (2.1) with

$$A = \begin{bmatrix} -1 & 3/2 \\ 1/3 & -1 \end{bmatrix},$$

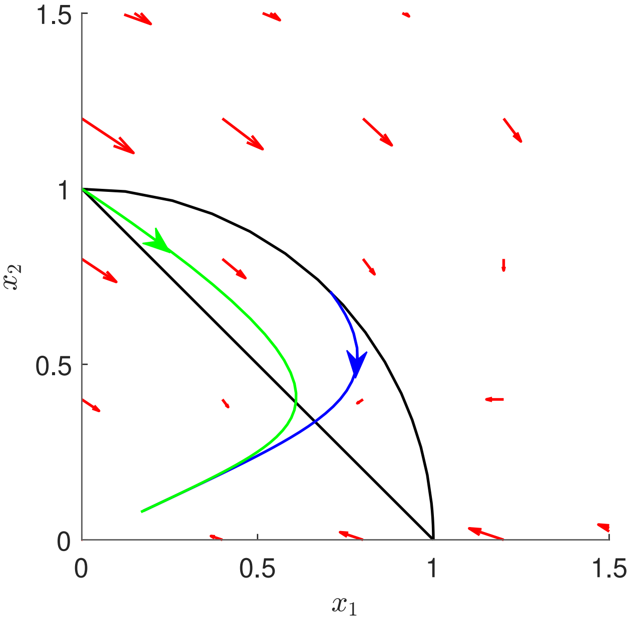


Figure 2. *The phase plane for system (2.1) with* $A = \left[\begin{smallmatrix} -1 & 3/2 \\ 1/3 & -1 \end{smallmatrix}\right]$*, which is reactive in* ℓ_1 *but not in* ℓ_2*. The line* $x_1 + x_2 = 1$ *and the circle* $x_1^2 + x_2^2 = 1$ *geometrically depict* $||x|| = 1$ *in the* ℓ_1 *and* ℓ_2 *norms, respectively. The derivative vectors for the phase plane are shown in red and two different initial trajectories are shown in green and blue. The green trajectory is an example that is reactive in* ℓ_1*, but not in* ℓ_2*, and the blue trajectory is another example that is not reactive in* ℓ_2*.*

where the phase plane is shown in Figure 2. Now the system is reactive in ℓ_1 ($\bar{\sigma}_1 > 0$) because if we start with one individual on the second patch (the dynamics governed by the second row of A), the total population grows, but in such a way that it will not be reactive in ℓ_2 ($\bar{\sigma}_2 \leq 0$). This example demonstrates that again reactivity in ℓ_2 can defy our biological expectation of reactivity, but now in the opposite way. Here the total population grows, yet the system is not reactive in ℓ_2. Note that this system is equivalent to system (3.2) with $\epsilon = 3$.

Together, the two examples highlight the differences that can occur when measuring reactivity in different norms and the caution that should be taken when interpreting reactivity in the ℓ_2 norm biologically. Here we only present examples that are reactive in ℓ_2 but not in ℓ_1 and vice versa but it is also possible to find examples of systems that attenuate in ℓ_2 but not in ℓ_1.

2.3. The relationship between stability and reactivity/attenuation. Now that we have presented two examples that demonstrate the difference between reactivity in the ℓ_1 and ℓ_2 norms, we show that in any norm if an equilibrium is asymptotically stable, it attenuates, and if an equilibrium is unstable, it is reactive.

Theorem 2.3. *If the* $x = 0$ *equilibrium for* $x'(t) = Ax(t)$ *is asymptotically stable and* A *is a Metzler matrix, then the system attenuates in any norm. Likewise if the* $x = 0$ *equilibrium* *is unstable, then the system is reactive in any norm.*

Proof. Let $\mu(A)$ be the eigenvalue of A with the largest real part. The matrix A is Metzler and so $\mu(A)$ is a real eigenvalue of A with an associated nonnegative eigenvector v (Theorem A.43 in [50]). The system with initial condition $x(0) = v$ then has a solution of the form $x(t) = e^{\mu(A)t}v$. Due to the absolute homogeneity property of all norms, $||x(t)|| = ||e^{\mu(A)t}v|| = |e^{\mu(A)t}|||v|| = e^{\mu(A)t}||v||$. Therefore, differentiating and setting $t = 0$ yields

$$\frac{1}{||x(t)||}\frac{d||x(t)||}{dt}\bigg|_{t=0} = \mu(A).$$

Now if the $x = 0$ equilibrium is asymptotically stable, then $\mu(A) < 0$ and therefore the minimum in the definition of $\underline{\sigma}_\omega$ (2.5) is negative so the system attenuates. If the $x = 0$ equilibrium is unstable, then $\mu(A) > 0$ and therefore the maximum in the definition of $\bar{\sigma}_\omega$ (2.2) is positive so the system is reactive. ■

In this section we have shown how to calculate reactivity and attenuation using the ℓ_1 norm in metapopulations, proven that if the equilibrium of a system is unstable/stable, then the system must be reactive/attenuate in any norm, and demonstrated the difference between reactivity in the ℓ_1 and ℓ_2 norms using two salient examples. We now return to the motivating feature of this paper—systems that are reactive and stable or attenuate and are unstable—and in the following section we provide examples of long lived transients in these systems.

3. Metapopulations with arbitrarily large transient growth or decay.

Here we examine two different metapopulations, one of which is reactive and can exhibit arbitrarily large transient growth, and the other that attenuates and can decline to arbitrarily small levels. In each case this transient growth differs from the system's long-term growth trajectory: the metapopulation that exhibits large growth eventually declines, and the system that declines eventually grows. Both of these example metapopulations are linear systems, and therefore the addition of nonlinearities to construct more realistic models could further exacerbate the length of the transient period. These examples are not meant to imply that there are realistic biological metapopulations that can grow arbitrarily large before decaying, but rather to emphasize that the difference between transient dynamics and asymptotic dynamics can be quite stark even in linear systems.

3.1. Arbitrarily large transient growth.

First we present a reactive metapopulation that can exhibit arbitrarily large transient growth, but eventually declines. In this metapopulation individuals can either give birth to new individuals on the same patch or give birth to individuals on the other patch, but there is no migration of individuals between patches. As mentioned in the introduction, this type of model is applicable to many marine metapopulations where adults are sedentary but larvae can disperse, to plant populations where seeds can be carried between habitat patches, or other populations governed by birth-jump processes. Let the metapopulation be described by

$$\begin{aligned} x' &= rx + b_{12}y, \\ y' &= b_{21}x + ry, \end{aligned} \tag{3.1}$$

so that r is the on patch birth rate minus the death rate, b_{12} is the birth rate of individuals on patch 2 producing new individuals on patch 1, and b_{21} is the birth rate of individuals on patch 1 producing new individuals on patch 2. The system is linear, so assuming that $r^2 \neq b_{12}b_{21}$ the only steady state is $x = y = 0$.

For the metapopulation to eventually decline, both eigenvalues need to be negative. For system (3.1) the eigenvalues are $r + \sqrt{b_{12}b_{21}}$ and $r - \sqrt{b_{12}b_{21}}$ and thus we require that $r < 0$ and $r^2 > b_{12}b_{21}$. Now in order for the metapopulation to be reactive in the ℓ_1 norm we need either $b_{12} > -r$ or $b_{21} > -r$. Here we choose $b_{21} > -r$, so that if we start with one individual on patch 1, i.e., $x(0) = 1$, $y(0) = 0$, the metapopulation initially grows.

To prove that the metapopulation can grow arbitrarily large, we show that the limit as some parameter approaches 0 of $\max_t(x(t) + y(t))$ is unbounded. Along with the initial condition $x(0) = 1$, $y(0) = 0$, this is equivalent to showing that the limit of the maximum amplification in the ℓ_1 norm, $\rho_{\max}$, becomes unbounded. This equivalence is because the initial growth rate for patch 1, λ_1, is greater than the initial growth rate for patch 2, λ_2, and thus by Lemma 2.1 and the linearity of the system, the maximum amplification will be achieved by the unit perturbation $x(0) = 1$, $y(0) = 0$. To take the limit, we must first reduce the parameters in our system until we are left with a single parameter that we can let approach 0, while still maintaining the inequalities above that govern the stability and reactivity of the system. Let $r = -1$, $b_{12} = \epsilon/2$, and $b_{21} = 1/\epsilon$, where ϵ is a small positive parameter that approaches 0. Our reduced system can now be written as

$$\begin{aligned} x' &= -x + \frac{\epsilon}{2}y, \\ y' &= \frac{1}{\epsilon}x - y, \\ x(0) = 1&, \qquad y(0) = 0. \end{aligned} \tag{3.2}$$

This system is stable and the digraph for this system is shown in Figure 3. This system is reactive in ℓ_1 and ℓ_2 for small ϵ and the solution is

$$x(t) = \frac{1}{2}\left(e^{-(1-\frac{1}{\sqrt{2}})t} + e^{-(1+\frac{1}{\sqrt{2}})t}\right), \tag{3.3}$$

$$y(t) = \frac{1}{\sqrt{2}\epsilon}\left(e^{-(1-\frac{1}{\sqrt{2}})t} - e^{-(1+\frac{1}{\sqrt{2}})t}\right). \tag{3.4}$$

For each fixed t, $\lim_{\epsilon\to 0} y(t) = \infty$, and thus the metapopulation can grow arbitrarily large. For further details, see Appendix B.

Therefore, even in a two-patch metapopulation that is asymptotically stable, there is always a parameter combination for which the total population, and thus also the maximum amplification in the ℓ_1 norm, $\rho_{\max}$, can initially grow arbitrarily large before they decay. This is not meant to imply that there are realistic biological metapopulations that can grow arbitrarily large before decaying, but to emphasize how different the transient and asymptotic dynamics of a system can be.

3.2. Transient decay to arbitrarily small levels. We now present an example of a metapopulation that attenuates and can decay to an arbitrarily small population size before eventually growing. We again use a metapopulation where individuals can either give birth to new

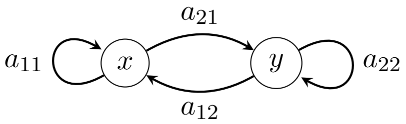


Figure 3. *General life cycle digraph for a two-patch model,* $\begin{bmatrix}x\\y\end{bmatrix}' = \begin{bmatrix}a_{11} & a_{12}\\a_{21} & a_{22}\end{bmatrix}\begin{bmatrix}x\\y\end{bmatrix}$. *The directed edges represent the birth rate of individuals on the outgoing patch producing new individuals on the incoming patch. The self loops are the birth rate minus the death rate on a patch. In system* (3.2), $a_{11} = -1$, $a_{12} = \epsilon/2$, $a_{21} = \epsilon^{-1}$, *and* $a_{22} = -1$. *In system* (3.5) $a_{11} = -1$, $a_{12} = \epsilon$, $a_{21} = \epsilon$, *and* $a_{22} = \epsilon$. *In system* (5.1) *if* $x_1 = x$ *and* $x_2 = y$, *then* $a_{11} = b_{11} - d_1$, $a_{12} = b_{12}$, $a_{21} = b_{21}$, *and* $a_{22} = b_{22} - d_2$.

individuals on their patch or on the other patch, but cannot migrate between patches. The difference between this metapopulation and the example used in the previous section is that now the on patch birth and death rates differ between patches, but the between patch birth rates are the same. Let the metapopulation be described by

$$\begin{aligned} x' &= r_1 x + \epsilon y, \\ y' &= \epsilon x + r_2 y, \end{aligned}$$

where r_1 is the birth rate minus the death rate on patch 1, r_2 is the birth rate minus the death rate on patch 2, and ϵ is the interpatch birth rate for both patches.

In order for the metapopulation to eventually grow, we assume that the birth rate is greater than the death rate on one of the patches. We choose this to be patch 2, and thus we require $r_2 > 0$. We also want our population to initially decline when starting on patch 1; for this to occur we assume $r_1 + \epsilon < 0$. To prove that the metapopulation can decay to an arbitrarily small population size we reduce the system to have a single parameter and then show that the limit as the parameter approaches 0 of $\min_t(x(t) + y(t)) = 0$. Let $r_1 = -1$ and $r_2 = \epsilon$, and then our system can be written in terms of a single positive parameter, ϵ, as

$$\begin{aligned} x' &= -x + \epsilon y, \\ y' &= \epsilon x + \epsilon y, \\ x(0) = 1&, \qquad y(0) = 0. \end{aligned} \tag{3.5}$$

This system is unstable and the corresponding digraph is shown in Figure 3. It attenuates in both the ℓ_1 and ℓ_2 norms for small ϵ.

It is possible to show that the minimum population size can grow arbitrarily small in a manner similar to the previous section, though the calculations are somewhat more complicated. Instead in this section, we perform an asymptotic expansion in terms of ϵ to demonstrate the limiting behavior of system (3.5). Let $x(t) = x_0(t) + \epsilon x_1(t) + O(\epsilon^2)$ and $y(t) = y_0(t) + \epsilon y_1(t) + O(\epsilon^2)$. Then the zero order system is

$$\begin{aligned} x_0'(t) &= -x_0(t), \\ y_0'(t) &= 0, \\ x_0(0) = 1&, \qquad y_0(0) = 0, \end{aligned}$$

which has the solution $x_0(t) = e^{-t}$ and $y_0 = 0$. We can proceed in a similar manner to solve the first order terms, and then our solution up to order ϵ is given by

$$\begin{aligned} x(t) &= e^{-t} + O(\epsilon^2), \\ y(t) &= \epsilon(1 - e^{-t}) + O(\epsilon^2). \end{aligned}$$

This solution is valid for small t and is therefore our inner approximation. To find our outer approximation for large t, we rescale $t = \tau/\epsilon$ and arrive at the system:

$$\begin{aligned} \epsilon X' &= -X + \epsilon Y, \\ \epsilon Y' &= \epsilon X + \epsilon Y. \end{aligned}$$

We can again solve the zero order and first order equations and arrive at the following solution with two undetermined coefficients:

$$\begin{aligned} X(\tau) &= \epsilon C e^{\tau} + O(\epsilon^2), \\ Y(\tau) &= C e^{\tau} + \epsilon(C\tau e^{\tau} + (C + K)e^{\tau}) + O(\epsilon^2). \end{aligned}$$

To solve our undetermined coefficients we require that $\lim_{t\to\infty} x(t) = \lim_{\tau\to 0} X(\tau)$ and $\lim_{t\to\infty} y(t) = \lim_{\tau\to 0} Y(\tau)$. From $x(\infty) = X(0^+)$, we find $C = 0$. Substituting $C = 0$ into $y(\infty) = Y(0^+)$ to solve for K we find $K = 1$. Adding our inner and outer solutions together and subtracting the overlap ($x(\infty) = X(0^+) = 0$ and $y(\infty) = Y(0^+) = \epsilon$) we find

$$\begin{aligned} x(t) &= e^{-t} + O(\epsilon^2), \\ y(t) &= \epsilon(e^{\epsilon t} - e^{-t}) + O(\epsilon^2), \end{aligned}$$

and thus our total population size behaves as

$$x(t) + y(t) = e^{-t} + \epsilon(e^{\epsilon t} - e^{-t}) + O(\epsilon^2). \tag{3.6}$$

We can see from (3.6) and Figure 4 that for very small ϵ, the total population size behaves similarly to e^{-t} before eventually growing. Thus for a minimum population threshold, we can always find an ϵ small enough, such that the solution crosses the threshold before the population grows. Alternatively, this can be proved by solving the full system and taking the minimum.

In this example the zero equilibrium is a saddle and as ϵ becomes arbitrarily small the initial condition becomes arbitrarily close to the stable manifold of the saddle. Therefore, the trajectory remains close to the stable manifold for a long time before heading toward the unstable manifold. The construction and dynamics of this example are thus qualitatively different from the previous example, where the zero equilibrium is stable and there is no unstable manifold present.

Here we have shown that there are metapopulations for which the transient population can grow arbitrarily large or small, no matter the asymptotic stability of the system. In the next section we demonstrate how increasing the patch number can increase transient growth in certain metapopulations.

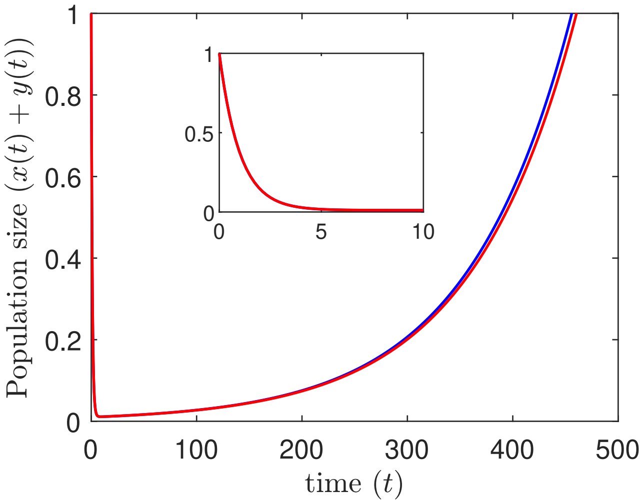


Figure 4. *Asymptotic approximation of the total population size (red) compared to the true total population size (blue) for system* (3.5)*, with* $\epsilon = 0.01$*. The asymptotic approximation is given by* (3.6)*.*

4. Increasing patch number increases transient timescale.

In this section we show how in certain scenarios increasing the number of habitat patches in birth-jump metapopulations can prolong the transient growth away from a stable equilibrium. In aquatic systems, habitat patches may be quite productive, but strong drift downstream can sweep most larvae to the next patch, leading to large transient growth on downstream patches before the population eventually disappears from the last patch. This phenomenon can occur in metapopulations situated in rivers, ocean channels, or reef systems where reefs are arranged along a coastline with a directional current. Here we explore how advection, or drift, can cause large transient growth in these metapopulations.

Consider a metapopulation on n patches where the dynamics are described by the following system of equations:

$$x' = Ax, \qquad x(0) = x_0, \tag{4.1}$$

$$A = \begin{bmatrix} r & \epsilon & 0 & \dots & 0 \\ b_2 & r & \epsilon & \ddots & \vdots \\ 0 & b_2 & r & \ddots & \\ \vdots & \ddots & \ddots & \ddots & \epsilon \\ 0 & \dots & 0 & b_2 & r \end{bmatrix},$$

where r is the birth rate minus the death rate on each patch, b_2 is the birth rate of patch $j-1$ on patch j, ϵ is the birth rate from patch $j+1$ to patch j, and x_0 is the initial population. The parameters b_2 and ϵ are positive and r is negative. The digraph for this system is shown in Figure 5.

The instantaneous measures of growth, λ_j, and reactivity in the ℓ_1 norm, $\bar{\sigma}_1$, are therefore $\lambda_1 = r + b_2$, $\lambda_j = r + b_2 + \epsilon$ for $j = 2, \dots, n-1$, $\lambda_n = r + \epsilon$, and $\bar{\sigma}_1 = r + b_2 + \epsilon$. Let $r + \epsilon < 0$

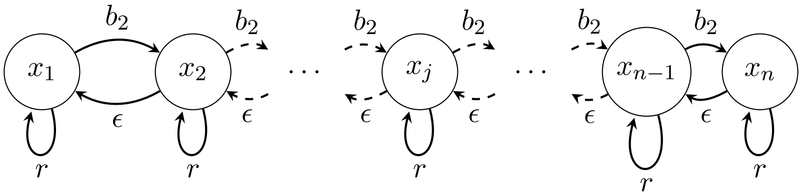


Figure 5. *Digraph for system (4.1). The directed edges represent the birth rate of individuals on the outgoing patch producing new individuals on the incoming patch. The self loops are the birth rate minus the death rate on a patch.*

and $r + b_2 > 0$, then the system is reactive ($\bar{\sigma}_1 > 0$), and this maximum initial growth rate is achieved if the initial population is all on any patch except for patch 1 or n, though if the initial population starts on patch 1 the initial growth rate is still positive. In system (4.1) A is a tridiagonal Toeplitz matrix, so it has eigenvalues [42]

$$\lambda_h = r + 2\sqrt{b_2\epsilon}\cos\left(\frac{h\pi}{n+1}\right), \qquad h = 1, \ldots, n,$$

and corresponding right eigenvectors, v_h, where the kth entry is given by

$$v_{h,k} = (b_2/\epsilon)^{k/2}\sin\left(\frac{hk\pi}{n+1}\right), \qquad k = 1, \ldots, n; h = 1, \ldots, n.$$

The solution to system (4.1), with initial condition $x_0 = e_1$, where e_1 is a vector with 1 in the first entry and 0*s* elsewhere, can therefore be written as

$$x(t) = We^{Jt}W^{-1}e_1,$$

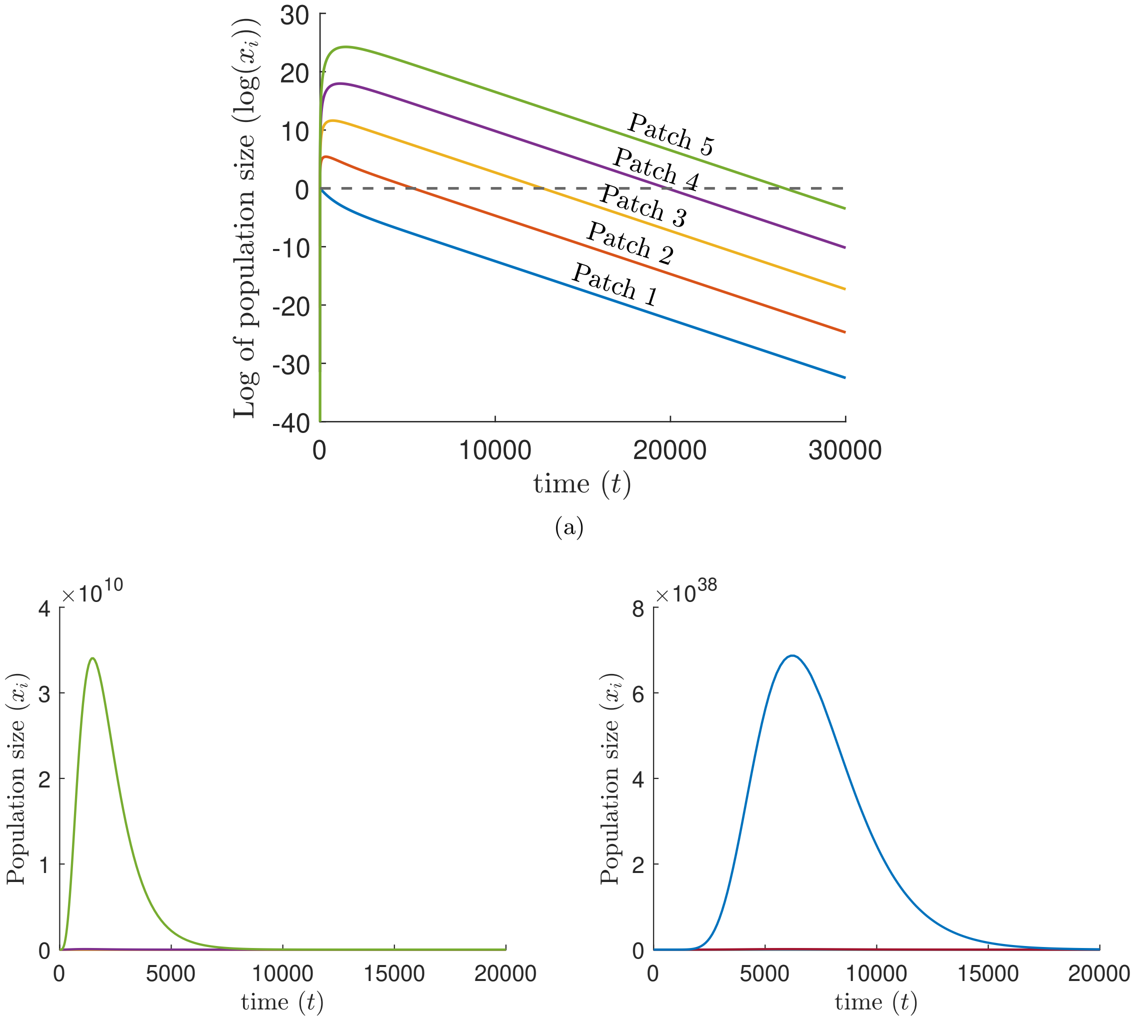
where W is a matrix containing the eigenvectors, v_h, and J is a diagonal matrix with the eigenvalues, λ_h, on the diagonal. For all but very small t the solution $x(t)$ is approximately equal to the amplification envelope in the ℓ_1 norm, $\rho(t)$, defined by (2.6). Through examination of the eigenvalues, this system is stable if ϵ is small enough such that $r+2\sqrt{b_2\epsilon} < 0$. Parameters that satisfy the inequalities that determine stability and reactivity in the ℓ_1 norm can be found in the caption of Figure 6. In this case the maximum total population size, and also maximum amplification, are given by

$$x_{\max} = \rho_{\max} = \max_{t\geq 0} 1^T We^{Jt}W^{-1}e_1,$$

with the corresponding time $t_{\max}$, which is the value of t for which the maximum occurs. The last measure of transience that is useful in this system is the total transient time, t_{total}, which we define as the time it takes for the population size to decline below one, after initially starting with one individual, or

$$t_{\text{total}} = \min\{t > 0 : 1^T We^{Jt}W^{-1}e_1 \leq 1\}.$$

So how does the number of patches affect the magnitude and length of transients? In Figure 6, which compares a 5 and 15 patch system, we can see that increasing the patch number increases both the magnitude of growth and the duration.



(a)

(b) (c)

Figure 6. *The population sizes on each patch for the advective system* (4.1) *with the initial condition* $x_0 = e_1$*, so that one individual is initially on patch* 1*. In* (a) *the population sizes are shown on a log scale for a metapopulation of* 5 *patches, and in* (b) *and* (c) *the population sizes are shown for a metapopulation of* 5 *and* 15 *patches, respectively. On the untransformed scale only the population size on the last patch can be seen as it is far larger than on any of the other patches, whereas on the log scale the population sizes of all patches can be seen. Parameters for this simulation are* $r = -0.00345$*,* $\epsilon = 0.000001$*, and* $b_2 = 2$*, chosen so that system* (4.1) *is reactive but stable.*

Here it can be difficult to see the duration of transience exhibited by all patches on a regular scale, but on the log scale we can see that all patches except for patch 1 experience a large period of transient growth, before they decay below 1 individual (Figure 6, dashed line). Patch 1 does not experience a large period of growth because the internal growth rate, r, is negative and the birth rate from patch 2 to patch 1, ϵ, is too small to overcome this negative internal growth rate.

What cannot be seen from Figure 6 is the dependence of transient growth on system parameters. We find that decreasing b_2 in system (4.1) results in a large decrease in the maximum population size (and maximum amplification), $x_{\max}$ (ρ_{max}), and the total transient time, t_{total}, but only a small decrease in the time at which the maximum population size is achieved, $t_{\max}$. Decreasing r, however, results in a large decrease in $x_{\max}$ ($\rho_{\max}$), $t_{\max}$, and t_{total}.

The relationship between increased transient time and number of patches can also be found for a linear metapopulation where all patches have negative initial growth rates, λ_j, except for the last patch, which has a positive initial growth rate. In this case the total population size decays for a long time before it eventually grows, and the time that it decays depends on the number of patches.

We can see then that for a linear metapopulation, the length of the linear array can accentuate the transient growth that is possible in the system and that this is especially true for advective systems where there is some sort of directed birth in one direction in the array. Systems with this type of advective flow include marine metapopulations located in channels near the mouth of rivers or long coral reefs that are captured inside of a dominant coastal current flow. To the best of our knowledge, this form of advection-driven transient has not been previously reported in the literature. However, related literature (e.g., [7]) models the effect of advection on population persistence and range shifts.

Having presented some illuminating metapopulation examples that demonstrate the magnitude that transient dynamics can differ from asymptotic dynamics, we now turn back to the general theory of transients in metapopulations and connect it to the source-sink classification of habitat patches.

5. Connecting the source-sink dynamics to the transient dynamics.

In this section we demonstrate how to connect the transient measures of initial population growth to the source-sink classification of habitat patches in the metapopulation, with a focus on marine metapopulations. There are several marine metapopulations for which habitat patches have been classified as sources or sinks [5, 49, 13] as defining the contribution of a habitat patch and the classification of habitat patches as sources or sinks is an important aspect in the design of marine reserves [14]. Here we connect the source-sink classification of a habitat patch to the transient dynamics that may occur if metapopulations are perturbed at low densities.

For the transient measure of the patch specific contribution to the initial growth of the total population we use λ_j, previously defined in section 2. To classify habitat patches as sources or sinks we use the next-generation matrix, K. Next-generation operators have previously been used to classify source and sink regions in heterogenous environments [29, 35, 25, 18]. In order to calculate the next-generation matrix for system (2.1) we decompose $A = F - V$, where F is a nonnegative matrix with positive entries that describe the birth of new individuals in the metapopulation, and V is a nonsingular M matrix [4] with entries that describe the transfer of individuals between compartments or in this case habitat patches, and also includes the death of individuals [54]. Examples 3, 4, and 5 illustrate the decomposition of A into F and V. Because V is a nonsingular M matrix, V^{-1} is nonnegative. The next-generation matrix, $K = [k_{ij}]$, can then be calculated as $K = FV^{-1}$ [54]. This next-generation matrix is then commonly used to calculate the basic reproduction number R_0, which is the average number of new individuals produced by one initial individual, and is defined as the spectral radius of K. However, we can also define R_j as the number of new individuals produced on all patches from one initial individual starting on patch j, which can then be calculated as

$$R_j = \sum_{i=1}^{n} k_{ij}.$$

We classify patch j as a *source* if $R_j > 1$, as then one individual on patch j would produce more than one individual in the total metapopulation. Likewise we classify patch j as a *sink* if $R_j < 1$, because in this case an individual cannot replace itself in the metapopulation. In the following sections we often refer to R_j as the source-sink classification of a habitat patch because while R_j is a number it can also be used to classify habitat patches as sources ($R_j > 1$) or sinks ($R_j < 1$).

5.1. Expressing R_0 as a weighted sum of R_j.

Before examining the connection between R_j and the initial growth λ_j, we first highlight a connection between R_j and R_0. It turns out, as shown in the following lemma, that R_0 can be calculated as a weighted sum of each R_j, and surprisingly this relationship between the spectral radius and the column sums of a matrix does not require any further assumptions on the matrix structure, though if the matrix is not nonnegative, the components of the right eigenvector need not be real. Here 1^T is the row vector with each entry equal to 1, and e_j is the vector with the only nonzero entry being 1 in the jth row.

Theorem 5.1. *Let $v = [v_i]$ be the right eigenvector associated with the dominant eigenvalue of the next-generation matrix, $\mathcal{R}_0$, normalized so $\sum_{1\le i\le n} v_i = 1$. Then the basic reproduction number $\mathcal{R}_0 = \sum_{1\le j\le n} R_j v_j$, where $R_j = 1^T K e_j = \sum_{i=1}^{n} k_{ij}$.*

Proof. First, we can rewrite $\mathcal{R}_0$ as

$$\mathcal{R}_0 = \mathcal{R}_0 1^T v = 1^T \mathcal{R}_0 v,$$

because the eigenvector has been normalized to sum to 1. Then, as $\mathcal{R}_0$ is the eigenvalue of K associated with v and the column sums of K are R_j,

$$\mathcal{R}_0 = 1^T \mathcal{R}_0 v = 1^T K v = \begin{bmatrix} R_1 & R_2 & \dots & R_n \end{bmatrix} v = \sum_{j=1}^{n} R_j v_j. \qquad \blacksquare$$

The entries v_j of the right eigenvector can be interpreted as the probability that a new individual begins on patch j [12]. Therefore, $\mathcal{R}_0$ can be interpreted as the sum over all patches, of the probability that an individual is born on patch j, multiplied by the number of new individuals it will produce on all other patches over its lifetime.

Similarly, if we define λ_0 to be the dominant eigenvalue of A, with the associated normalized eigenvector u, then

$$\lambda_0 = 1^T A u = \sum_{j=1}^{n} \sum_{i=1}^{n} a_{ij} u_j = \sum_{j=1}^{n} \lambda_j u_j,$$

where it should be noted that λ_j is the jth column sum of A, rather than an eigenvalue of A.

5.2. Connecting the source-sink classification, R_j, to the initial growth rate, λ_j.

Now that we have decomposed the dominant eigenvalues, R_0 and λ_0, into weighted sums of the columns of K and A, respectively, we proceed to connect the source-sink classification of a particular patch, R_j, to the initial growth from an individual on that patch, λ_j. To do so there are some restrictions that we need to impose on our metapopulation system and this is where we limit our study to marine or birth-jump metapopulation models where juveniles or seeds can disperse between patches while adults remain confined to habitat patches. The mathematical restriction defined by this class of models comes from the decomposition of A into $F - V$. Here V contains all entries that describe the transfer of individuals between compartments or patches. For the results presented in this section, we require that V has the following reducible form:

$$V = \begin{bmatrix} V_{11} & 0 \\ V_{21} & D \end{bmatrix},$$

where V_{11} is $k \times k$, $D = \text{diag}(d_{k+1}, \dots, d_n)$ with $d_{k+1}, \dots, d_n$ all positive, $0 \le k \le n-1$, and V is a nonsingular M matrix.

With this structure, individuals on patches $j = k+1, \dots, n$ cannot migrate between patches, but can still give birth to new individuals on any patch. Under this structure, we first present proofs connecting our instantaneous and generational growth measures, λ_j and R_j, before presenting a two-patch example. If V is completely diagonal, then there is no migration between any patches, only birth on other patches. This is the case for models of plants with seed dispersal, or simplified marine metapopulation models if the juvenile stage is not explicitly modelled.

Theorem 5.2. *Let $A = F - V$ for system (2.1), where F is nonnegative, and V is a nonsingular M matrix with the following form:*

$$V = \begin{bmatrix} V_{11} & 0 \\ V_{21} & D \end{bmatrix},$$

where V_{11} is $k \times k$, $D = \text{diag}(d_{k+1}, \dots, d_n)$ with $d_{k+1}, \dots, d_n$ all positive, and $0 \le k \le n-1$. For $k+1 \le j \le n$, λ_j is positive if and only if $R_j > 1$.

Proof. First, we can write λ_j as

$$\lambda_j = \sum_{i=1}^{n} a_{ij} = 1^T A e_j.$$

Then decomposing A into $F - V$, and inserting $V^{-1}V$,

$$\lambda_j = 1^T(F-V)e_j = 1^T(F-V)V^{-1}Ve_j = 1^T(FV^{-1} - I)Ve_j.$$

For $k+1 \le j \le n$, V is diagonal, so $Ve_j = d_j e_j$. Therefore,

$$\lambda_j = 1^T(FV^{-1} - I)d_j e_j = (R_j - 1)d_j.$$

Now $d_j > 0$, and thus $\lambda_j > 0$ if and only if $R_j > 1$. ■

Corollary 5.3. *In the notation of Theorem 5.2, if V is diagonal, then $\lambda_j > 0$ if and only if $R_j > 1$ for $j = 1, \ldots, n$.*

Corollary 5.4. *Under the same conditions as Theorem 5.2, $\bar{\sigma}_1 > 0$ if $\max_{k+1\le j\le n} R_j > 1$, and $\underline{\sigma}_1 < 0$ if $\min_{k+1\le i\le n} R_i < 1$.*

Proof. Under the conditions in Theorem 5.2, we know that $R_j - 1$ has the same sign as λ_j for $k+1 \le j \le n$. Therefore, if $\max_{k+1\le j\le n} R_j > 1$, then $\bar{\sigma}_1 = \max_{1\le j\le n} \lambda_j > 0$, i.e., the system is reactive. Similarly if $\min_{k+1\le j\le n} R_j < 1$, then $\underline{\sigma}_1 = \min_{1\le j\le n} \lambda_j < 0$, i.e., the population attenuates. ■

Corollary 5.5. *Under the same conditions of Theorem 5.2, only with V diagonal, then $\bar{\sigma}_1 > 0$ if and only if $\max_{1\le j\le n} R_j > 1$ and $\underline{\sigma}_1 < 0$ if and only if $\min_{1\le j\le n} R_j < 1$.*

Proof. From Corollary 5.3, $\lambda_j > 0$ if and only if $R_j > 1$ for each patch j. Therefore, if $\bar{\sigma}_1 = \max_{1\le j\le n} \lambda_j > 0$, then $\max_{1\le j\le n} R_j > 1$, and likewise if $\max_{1\le j\le n} R_j > 1$, then $\bar{\sigma}_1 > 0$. The same argument holds for $\min_{1\le j\le n} \lambda_j$ and $\min_{1\le j\le n} R_j$. ■

Now that we have presented theory connecting the initial growth rate, λ_j, to the source-sink classification of patch, R_j, we present an example to illustrate how to calculate these growth rate and source-sink measures and how Theorem 5.2 and Corollaries 5.3 and 5.5 can be used to connect them.

Example 3. Here we present an example of a metapopulation consisting of two habitat patches, patch 1 and patch 2. New individuals can be born on either patch, but no individuals can migrate between patches. This system represents a simplification of the adult dynamics of many marine meroplanktonic metapopulations, where dispersal between patches occurs at the larval stage, rather than the sedentary adult stage. This system could also represent plant metapopulations that spread through seed dispersal, if the habitat landscape is patchy. The metapopulation dynamics can be represented with the following set of ODEs:

$$\begin{aligned} x_1' &= b_{11}x_1 + b_{12}x_2 - d_1x_1, \\ x_2' &= b_{21}x_1 + b_{22}x_2 - d_2x_2, \end{aligned} \tag{5.1}$$

where b_{ij} is the birth rate for births from patch j to patch i, and d_i is the death rate on patch i. The lifecycle graph for this system is shown in Figure 3.

We then decompose $A = F - V$ and construct the next-generation matrix, $K = FV^{-1}$:

$$A = \begin{bmatrix} b_{11} - d_1 & b_{12} \\ b_{21} & b_{22} - d_2 \end{bmatrix}, \quad F = \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}, \quad V = \begin{bmatrix} d_1 & 0 \\ 0 & d_2 \end{bmatrix},$$
$$K = FV^{-1} = \begin{bmatrix} b_{11}/d_1 & b_{12}/d_2 \\ b_{21}/d_1 & b_{22}/d_2 \end{bmatrix}.$$

For an initial individual starting on patch 1, the expected lifetime is $1/d_1$, and the rate that the individual is producing new individuals on both patches is $b_{11} + b_{21}$. Therefore, $R_1 = (b_{11} + b_{21})/d_1$ is the total number of individuals born onto both patch 1 and patch 2 over one generation. It is clear that $\lambda_1 = b_{11} + b_{21} - d_1 > 0$ if and only if $R_1 = \frac{b_{11}}{d_1} + \frac{b_{21}}{d_1} > 1$, in accordance with Corollary 5.3. Similarly $\lambda_2 = b_{12} + b_{22} - d_2 > 0$ if and only if $R_2 = \frac{b_{12}}{d_2} + \frac{b_{22}}{d_2} > 1$. The system is therefore reactive if $\max(R_1, R_2) > 1$ (Corollary 5.5).

At first glance it seems obvious that if an individual starts on a source patch the population should have a positive initial growth rate or if the population starts on a sink patch it should have a negative initial growth rate, and we have shown from Corollary 5.3 and Example 3 that this is indeed the case for marine metapopulations. What is perhaps surprising is that this is not the case for general metapopulations when adults can migrate between habitat patches, and thus when the conditions of Theorem 5.2 and Corollary 5.3 are not met. In the general case it is possible to start with an individual on a source patch, but for the population to initially decline, and likewise to start on a sink patch, but for the population to initially grow. An example of such a metapopulation is shown in Appendix A.

Here in this section we have shown that for marine metapopulations and other metapopulations where the population dynamics are defined by birth-jump processes, there is a one-to-one relationship between the source-sink classification of a patch and the initial growth rate when starting with one adult on a patch. That is, the initial population growth rate is positive if we start with one adult on patch j if and only if patch j is a source, and the initial growth rate is negative if and only if patch j is a sink. This is a useful relationship biologically as there are several marine metapopulations where patches have already been classified into sources and sinks, and thus the transient dynamics for these systems can now be better understood.

6. Stage structure.

In this section we add stage structure to demonstrate some of the nuances in analyzing transients in stage structured metapopulation models. The main issue with analyzing reactivity and attenuation in models with stage structure is due to the fact that adults often give birth to many more juveniles than will survive to become adults, and that juveniles cannot normally give birth to new juveniles. This presents a few complications.

The first complication is the fact that if we want to analyze the initial growth or decay of a population, starting with an individual in a patch, it now depends if the individual is a juvenile or an adult. If we start with a juvenile, then there is no way that the total population, or even the patch population, can grow, given that the juvenile has to first survive to the adult stage to give birth to new juveniles. Thus we want to start with one adult on a patch.

However, if we start with an adult in a patch, and it gives birth to new juveniles, how do we count these new juveniles? If we are considering a marine metapopulation do we count every larvae as a new individual? If so, every marine metapopulation would exhibit transience, as each adult often produces thousands of larvae. This then begs the following question: in a stage structured metapopulation, can we scale the juvenile population so that transient measures of population growth, such as reactivity and attenuation, are useful for stage structured models and measure the biologically relevant quantities?

To motivate the necessity of an honest scaling we highlight a discrete time example of transients in Dungeness crabs from Caswell and Neubert [9]. Dungeness crabs give birth to an enormous number of larvae, many of which do not survive to settle and become juveniles after one year. In this case the discrete time model requires a census time to measure new crabs after one year. If the census is taken prebreeding, then the system exhibits little reactivity, as many of the larvae that were initially born have not survived to become one-year-old juveniles. However, if the census is taken postbreeding, then all of the eggs or larvae are counted and the initial amplification is increased by 10^5. The models considered in this paper are continuous time and do not face this exact problem, but it is easy to see that the addition of a larvae stage in a marine stage structured metapopulation has large effects on the reactivity of the system.

Returning then to our stage structured model with only juvenile and adult stages, how should the juvenile stage be scaled so that an initial growth in juveniles also corresponds in some sense to growth in the total population? Ideally, we would scale the juvenile population so that each juvenile is scaled by the probability that it will become an adult. If we scale our population in this way then the measures of reactivity and attenuation regain their original meaning. If the maximum initial growth rate of our population, now scaled to be in terms of adults, is positive, then our system is reactive, and if the minimum is negative, then it attenuates.

A biologically relevant measure of reactivity in a stage structured model must then be focused on the initial growth rate of the population, calculated so that the growth rates of juveniles are scaled by their contribution to the adult population. Under this scaling if any adult on any habitat patch produces many juveniles, but less than one become viable adults, then such a metapopulation is not reactive. Whereas if there is a patch such that one adult produces many juveniles and more than one survive to adulthood, then the metapopulation is reactive, because the stage structured population, where juveniles are scaled according to their contribution to the adult population, is growing.

In the following sections we formally define such a scaling using a weighted ℓ_1 norm and contrast it with the unweighted ℓ_1 norm that we have previously been using to calculated reactivity in metapopulations without stage structure.

6.1. Unweighted ℓ^1.

We want to measure reactivity and attenuation as the total initial growth rate of the population, measured using either the weighted or unweighted norm, when we start with one adult on a patch. We first present the unweighted ℓ^1 measure of the initial growth rate to demonstrate the mathematical framework that we use to examine reactivity in a stage-structured population with juveniles and adults.

Consider a population with juvenile and adult stages on n patches. Let the population dynamics be described by

$$x'(t) = Ax(t), \tag{6.1}$$

where A is a $2n \times 2n$ matrix, arranged so that all ODEs describing the change in the adult populations are in rows $n+1$ to $2n$. Decompose A into $A = F - V$, where F is nonnegative with positive entries that describe the birth of new individuals in the metapopulation, and V is a nonsingular M matrix [4] (V^{-1} is nonnegative) with entries that describe the transfer of individuals between compartments or in this case habitat patches, and also includes the death of individuals [54]. We are interested in metapopulations where adults can give birth to juveniles, but juveniles cannot give birth to new juveniles, so F and V can be written in block form as follows:

$$F = \begin{bmatrix} 0 & F_{12} \\ 0 & 0 \end{bmatrix}, \quad V = \begin{bmatrix} V_{11} & 0 \\ V_{21} & V_{22} \end{bmatrix}. \tag{6.2}$$

With this decomposition F_{12} contains all the new juvenile births from each adult patch, V_{11} is a diagonal matrix that contains the rates of juvenile mortality on each patch as well as the maturation from juveniles to adults, V_{22} is a diagonal matrix that contains the rates of adult mortality on each patch, and V_{21} contains the negative of the rates of maturation/migration from juveniles to adults.

We define $\tilde{\lambda}_j$ to be the initial population growth rate, starting with one adult on patch j, measured using the ℓ_1 norm. This can be defined mathematically for $1 \leq j \leq n$ as

$$\tilde{\lambda}_j = \underbrace{\sum_{i=1}^{n} x_i'(0)}_{\text{juvenile}} + \underbrace{\sum_{i=n+1}^{2n} x_i'(0)}_{\text{adult}}, \quad x(0) = e_{j+n}.$$

In terms of F and V

$$\tilde{\lambda}_j = \sum_{i=1}^{n} f_{12ij} - \sum_{i=1}^{n} v_{22ij},$$

where f_{12ij} and v_{22ij} are the (i,j) entries of F_{12} and V_{22}, respectively.

We use the tilde to differentiate the initial growth rate in the stage structured population, where we specifically begin with one adult on a patch, from the initial growth rate in a population without stage structure, where there is no difference in the type of individual that we start with. Having presented the mathematical framework that we use to measure reactivity in a stage structured population using the unweighted ℓ_1 norm, we now use a weighted ℓ_1 norm that better captures the biological meaning of reactivity.

6.2. Weighted ℓ^1 for each patch.

In order to measure reactivity in a biologically meaningful fashion, we introduce a new measure of the initial population growth rate, $\tilde{\lambda}_j^p$. This initial population growth rate is calculated using a weighted ℓ_1 norm so that the adult population is still measured using the regular ℓ_1 norm, but the juvenile population on each patch is scaled by the probability that the juveniles survive to adulthood; the patch specific nature of the weighing is why we denote the initial growth rate $\tilde{\lambda}_j^p$. In this fashion $\tilde{\lambda}_j^p$ measures the initial growth rate of the total population if every member of the metapopulation was weighted according to how much they will contribute to the adult population. Adults are therefore not weighted, and juveniles are weighted by the probability that they survive to adulthood. This weighting recaptures the biological meaning of reactivity, where a system will only be reactive if the adult population will grow, and a system will not be reactive if there is only an initial spike in the juvenile population.

We use the same framework as in the previous section to mathematically calculate $\tilde{\lambda}_j^p$, where we decompose $A = F - V$ and F and V are shown in block form in (6.2). Then we weight the juvenile population growth on each patch i by a factor s_i, where s_i is the probability that a juvenile from patch i eventually becomes an adult. From the block form V, s_i can be calculated as

$$s_i = \sum_{k=1}^{n} (-V_{21} V_{11}^{-1})_{ki}. \tag{6.3}$$

To see how this corresponds to the probability of survival of a juvenile on patch i, consider the different block components of F and V. The matrix V_{11}^{-1} is diagonal, with the (j,j) entry representing the average residence time of a juvenile born onto patch j. The matrix $-V_{21}$ contains the rates of maturation/migration of juveniles becoming adults on different patches, so the (i, j) entry is the rate of maturation/migration of a juvenile on patch j becoming an adult on patch i. This means that when we multiply $-V_{21}$ by V_{11}^{-1} we are multiplying each of these rates by the residence times of the juveniles in the appropriate patches. In this way, the (i, j) entry of $-V_{21}V_{11}^{-1}$ is then the probability that a juvenile leaving patch j arrives on patch i. Therefore, the jth column sum of $-V_{21}V_{11}^{-1}$ is the probability that a juvenile starting on patch j becomes an adult on any other patch.

The initial growth rate using the weighted norm, $\tilde{\lambda}_j^p$, can then be calculated as the sum of the juvenile growth rates, each multiplied by the patch specific survival s_i, and the adult growth rates. Mathematically, this is defined as

$$\begin{aligned}\tilde{\lambda}_j^p &= \underbrace{\sum_{i=1}^{n} s_i x_i'(0)}_{\text{juvenile}} + \underbrace{\sum_{i=n+1}^{2n} x_i'(0)}_{\text{adult}}, \quad x(0) = e_{j+n}\\ &= \sum_{i=1}^{n} s_i f_{12ij} - \sum_{i=1}^{n} v_{22ij}.\end{aligned}$$

In order to demonstrate that the initial growth rate calculated using the weighted ℓ_1 norm, $\tilde{\lambda}_j^p$, indeed measures the growth rate of the population if all individuals are weighted according to their contribution to the adult population, we show that $\tilde{\lambda}_j^p$ is equivalent to scaling the juvenile population on each patch by the probability of survival to adulthood, and then measuring the initial growth rate using the unweighted ℓ_1 norm, defined previously as $\tilde{\lambda}_j$.

Theorem 6.1. *If each juvenile population in system (6.1) is rescaled by the patch specific survival probability, $s_i = \sum_{k=1}^{n}(-V_{21}V_{11}^{-1})_{ki}$, then the initial growth rate using the unweighted ℓ^1 norm, $\tilde{\lambda}_j$, is equal to the patch specific weighted initial growth rate, $\tilde{\lambda}_j^p$, for the unscaled system.*

Proof. Rescale the juvenile population on patch i by the patch specific survival probability s_i given in (6.3). In terms of system (6.1) this means that $x_i^* = s_i x_i$ for $i = 1, \ldots, n$, $x_i^* = x_i$ for $i = n + 1, \ldots, 2n$. Rewrite the system of equations

$$x^{*\prime} = A^* x^*,$$

$$A^* = F^* - V^*, \quad F^* = \begin{bmatrix} 0 & SF_{12} \\ 0 & 0 \end{bmatrix}, \quad V^* = \begin{bmatrix} V_{11} & 0 \\ V_{21}S^{-1} & V_{22} \end{bmatrix},$$

where $S = \mathrm{diag}(s_1, \ldots, s_n)$. The unweighted initial growth rate for the scaled system is then

$$\tilde{\lambda}_j^* = \sum_{i=1}^{n}(SF_{12})_{ij} - \sum_{i=1}^{n} v_{22ij} = \sum_{i=1}^{n} s_i f_{12ij} - \sum_{i=1}^{n} v_{22ij} = \tilde{\lambda}_j^p.$$

Thus the unweighted initial growth rate for the scaled system is equal to the patch-weighted initial growth rate of the unscaled system, $\tilde{\lambda}_j^p$. ■

We believe that it is more intuitive to measure reactivity in a stage-structured system using a weighted norm, rather than scaling the juvenile population and using the unweighted ℓ_1 norm, but for other systems this may not be the case. Recently Mari et al. [34] have developed a new measure of reactivity called generalized reactivity, or g-reactivity, so that the reactivity of any specific combination of state variables in a system can be measured, and we demonstrate how to place our work in this context. The general framework of g-reactivity allows the reactivity of only the predator to be measured in a predator-prey system, or a single patch in a metapopulation model. Moreover, in a stage-structured model, g-reactivity can be used to allow for a differential contribution of the juvenile and adult populations to the reactivity of the system, and so we can compare the calculation of g-reactivity to our calculation using the weighted ℓ_1 norm. To calculate the g-reactivity of a system $x' = Ax$, a linear transformation is introduced, $y = Cx$, where C is a matrix that defines the required contribution of each of the state variables, and then reactivity is calculated for y using equation (2.2). For system (6.1), if C is a $2n \times 2n$ identity matrix, but with the first n diagonal entries replaced with $s_1, \ldots, s_n$, then g-reactivity is the ℓ_2 norm equivalent of reactivity under our weighted ℓ_1 norm, $\max_j \tilde{\lambda}_j^p$.

Returning to our measure of initial growth rate using a patch weighted norm, we present two examples below to illustrate the calculation of $\tilde{\lambda}_j^p$ in different systems.

Example 4. Consider a two-patch system where juveniles are born onto all patches but only mature into adults on the patch where they were born:

$$
\begin{aligned}
j_1' &= b_{11}a_1 + b_{12}a_2 - m_1 j_1 - d_{j1} j_1,\\
j_2' &= b_{21}a_1 + b_{22}a_2 - m_2 j_2 - d_{j2} j_2,\\
a_1' &= m_1 j_1 - d_a a_1,\\
a_2' &= m_2 j_2 - d_a a_2.
\end{aligned}
\tag{6.4}
$$

Here j_i is the number of juveniles on patch i, a_i is the number of adults on patch i, b_{ik} is the birth rate of juveniles on patch i from adults on patch k, m_i is the maturation rate of juveniles on patch i into adults on patch i, d_{ji} is the death rate of juveniles on patch i, and d_a is the death rate of adults, which is the same on both patches. The lifecycle graph for this system is shown in Figure 7.

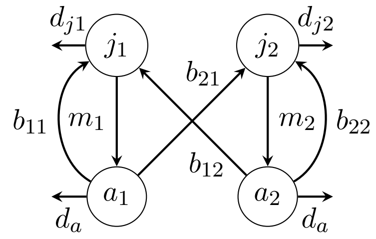


Figure 7. *Digraph for system (6.4). Here b_{ik} is the birth rate of juveniles on patch i from adults on patch k, m_i is the maturation rate of juveniles on patch i to adults on patch i, d_{ji} is the death rate of juveniles on patch i, and d_a is the death rate of adults.*

In this case

$$F_{12} = \begin{bmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{bmatrix}, \quad V_{11} = \begin{bmatrix} m_1 + d_{j1} & 0 \\ 0 & m_2 + d_{j2} \end{bmatrix}, \quad V_{21} = \begin{bmatrix} -m_1 & 0 \\ 0 & -m_2 \end{bmatrix},$$

$$V_{22} = \begin{bmatrix} d_a & 0 \\ 0 & d_a \end{bmatrix}, \quad -V_{21}V_{11}^{-1} = \begin{bmatrix} \frac{m_1}{m_1+d_{j1}} & 0 \\ 0 & \frac{m_2}{m_2+d_{j2}} \end{bmatrix},$$

$$\tilde{\lambda}_1^p = s_1 b_{11} + s_2 b_{21} - d_a, \quad \tilde{\lambda}_2^p = s_1 b_{12} + s_2 b_{22} - d_a,$$

$$s_1 = \frac{m_1}{m_1 + d_{j1}}, \quad s_2 = \frac{m_2}{m_2 + d_{j2}}.$$

If we look at $\tilde{\lambda}_1^p$, we see that s_1 is the probability that a juvenile born onto patch 1 survives to become an adult and it is multiplying b_{11}, the birth rate of juveniles onto patch 1 from adults on patch 1. Therefore, the first component of $\tilde{\lambda}_1^p$ represents the rate of birth of new juveniles onto patch 1 from one adult on patch 1, but scaled by the probability that these juveniles survive to become adults. Likewise the second component, $s_2 b_{21}$, is the rate of birth of new juveniles onto patch 2 from one adult on patch 1, scaled by the probability that those juveniles also become adults. Thus $\tilde{\lambda}_1^p$ is the initial growth rate of the total population, scaled in terms of the contribution to the adult population, when the population begins with one adult on patch 1.

Example 5. We also consider a system in which juveniles are born onto the same patch as adults, but can then migrate between patches as they mature into adults (shown in Figure 8),

$$\begin{aligned} j_1' &= b_{11}a_1 - m_{11}j_1 - m_{21}j_1 - d_{j1}j_1, \\ j_2' &= b_{22}a_2 - m_{22}j_2 - m_{12}j_2 - d_{j2}j_2, \\ a_1' &= m_{11}j_1 + m_{12}j_2 - d_a a_1, \\ a_2' &= m_{22}j_2 + m_{21}j_1 - d_a a_2, \end{aligned} \tag{6.5}$$

from which we calculate

$$F_{12} = \begin{bmatrix} b_{11} & 0 \\ 0 & b_{22} \end{bmatrix}, \quad V_{11} = \begin{bmatrix} m_{11} + m_{21} + d_{j1} & 0 \\ 0 & m_{12} + m_{22} + d_{j2} \end{bmatrix}, \quad V_{21} = \begin{bmatrix} -m_{11} & -m_{12} \\ -m_{21} & -m_{22} \end{bmatrix},$$

$$V_{22} = \begin{bmatrix} d_a & 0 \\ 0 & d_a \end{bmatrix}, \quad -V_{21}V_{11}^{-1} = \begin{bmatrix} \frac{m_{11}}{m_{11}+m_{21}+d_{j1}} & \frac{m_{12}}{m_{12}+m_{22}+d_{j2}} \\ \frac{m_{21}}{m_{11}+m_{21}+d_{j1}} & \frac{m_{22}}{m_{12}+m_{22}+d_{j2}} \end{bmatrix},$$

$$\tilde{\lambda}_1^p = s_1 b_{11} - d_a, \quad \tilde{\lambda}_2^p = s_2 b_{22} - d_a,$$

$$s_1 = \frac{m_{11} + m_{21}}{m_{11} + m_{21} + d_{j1}}, \quad s_2 = \frac{m_{12} + m_{22}}{m_{12} + m_{22} + d_{j2}}.$$

Now if we examine the first component of $\tilde{\lambda}_1^p$, $s_1 = (m_{11} + m_{21})/(m_{11} + m_{21} + d_{j1})$, we can see that because juveniles from patch 1 can now migrate (as they mature) to both patches, s_1 is the probability that juveniles from patch 1 become adults on either patch. Likewise s_2 is the probability that juveniles from patch 2 become adults on either patch. Biologically we are scaling the birth rate on a patch by the probability that a juvenile survives to adulthood on any patch.

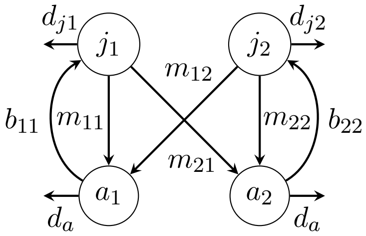


Figure 8. *Digraph for system (6.5). Here b_{ii} is the birth rate of juveniles on patch i from adults on patch i, m_{ik} is the maturation rate of juveniles on patch k to adults on patch i, d_{ji} is the death rate of juveniles on patch i, and d_a is the death rate of adults.*

Here we have shown that if we use a weighted ℓ_1 norm to scale the initial growth rate so that the juvenile population is scaled by the patch specific probability that juveniles become adults, then our scaled initial growth rate, $\tilde{\lambda}_j^p$, matches the biological intuition that we would like when measuring initial growth of the population. It is positive if the population, scaled so that every individual is measured by its contribution to the adult population, is growing, and negative if the population is decreasing. Measures of reactivity and attenuation then also represent their intuitive biological properties, and we are no longer in the situation (as if the initial growth rate was unscaled) that most marine metapopulations are reactive.

It is also possible to create a weighted norm where the juvenile populations on each patch are weighted by the same probability of survival, rather than by patch-specific probabilities s_i. In some cases it may be useful to scale all patches by the same survival probability, though under this weighted norm reactivity no longer corresponds exactly to the intuitive biological meaning mentioned previously.

7. Discussion.

Transient dynamics often differ drastically from the asymptotic dynamics of a system and require different analytical tools. In this paper we have presented a framework for analyzing transient dynamics in birth-jump metapopulations, from the choice of norms to the incorporation of stage structure. We began by using the ℓ_1 norm to define reactivity and attenuation in single species metapopulations and used examples to compare reactivity in the ℓ_1 norm with reactivity in the more commonly used ℓ_2 norm. We presented two models that gave rise to long transients: one stable system that exhibits a long period of growth before eventual decay and one unstable system that exhibits a long period of decay before growth. In birth-jump metapopulations, where patches are connected via larval dispersal, we showed how strong advective flow, coupled with a large number of patches, can lead to large transient growth. We believe that this could be a key new mechanism giving rise to transient dynamics in marine metapopulations where habitat patches are found in a linear array, such as salmon farms along a fjord (see, for example, [18]). We then connected the initial growth rate of the metapopulation to the source-sink classification of patches, and last we demonstrated how to measure reactivity meaningfully in stage-structured marine metapopulations.

We are by no means the first to analyze the transient dynamics of systems, and in fact there has been an increase in the study of transient dynamics over the last few decades. In a pair of recent papers, several authors have identified mechanisms as the main causes of long transients in ecological systems [21, 36]. These identified mechanisms that cause the long transients present in the examples in this paper are slow-fast systems, crawl-bys, and high dimensionality. Slow-fast systems cause long transients when the system rapidly converges to a slow manifold, then moves slowly toward or away from an equilibrium, depending on the stability of the system. This occurs in both examples in section 3. The second example in section 3 is also an instance of a crawl-by where the initial perturbation is near a saddle equilibrium but the movement away from the equilibrium occurs over a long timescale. Last, in section 4 we explicitly demonstrated how increasing the dimension of a system, by increasing the patch number in a linear metapopulation, leads to longer transients.

Our work also reinforces the fact that reactivity is a property specific to the norm under which it is measured. This has been mentioned in the first paper on reactivity by Neubert and Caswell [39], who also recognize that it is always possible to find a norm such that a stable system is never reactive. It has also been noted by Lutscher and Wang [33], who mention that reactivity must be analyzed in the dimensional version of a system rather than the nondimensionalized version. The reactivity may be different between the two systems but the dimensional system is where the measure of reactivity is biologically meaningful. When analyzing reactivity in metapopulations this fact is significant in two ways: first by using the ℓ_1 norm rather than the ℓ_2 norm to measure reactivity we can explicitly measure the growth rate of a population, and second by using a weighted ℓ_1 norm we prevent the juvenile population from disproportionately affecting the reactivity of the system.

Differentially weighting certain classes of a population to calculate reactivity has been mentioned in passing by Verdy and Caswell [55], and more extensively by Mari et al. [34], who developed a new measure of reactivity called general reactivity, or g-reactivity. This is a method of only measuring the reactivity of the components of interest in a population, e.g., predators in a predator-prey model, and can also be used more generally to scale the contribution of different components of the population. Our method of using a weighted ℓ_1 norm for stage-structured models has an equivalent formulation using g-reactivity that is discussed in subsection 6.2, though Mari et al. [34] use the ℓ_2 norm to measure reactivity, rather than the ℓ_1 norm, and are thus using a different measure of population growth.

While we believe the ℓ_1 norm is the most biologically relevant norm to measure reactivity, we are among the first to use it to analyze reactivity in continuous time models. Townley et al. [52] show how to calculate reactivity for stage-structured models in continuous time using the ℓ_1 norm, but in following papers proceed to analyze reactivity in the ℓ_1 norm only in discrete time systems [53, 47, 48]. Most authors measure reactivity with the ℓ_2 norm, presumably due to the nice mathematical property that reactivity in the ℓ_2 norm is given simply as the maximum eigenvalue of $(A + A^T)/2$ [39, 9, 40, 41, 55, 33, 46]. But while mathematically tractable, the biological meaning of Euclidean distance (ℓ_2) is less clear than population size (ℓ_1) and as shown in subsection 2.2, there are times when reactivity in ℓ_2 does not correspond to an increase in population size.

The reactivity of an equilibrium can also be understood geometrically, as shown in Figures 1 and 2. Under the ℓ_1 norm the zero equilibrium of a single species metapopulation (2.1) is reactive if the dot product of the derivative vector of any initial perturbation and the outward normal vector of the plane $x_1 + x_2 + \ldots x_n = 1$ is positive. This geometric interpretation is applicable when the matrix A describing the dynamics of the linearized system, $x'(t) = Ax(t)$, is Metzler. If instead we want to examine the reactivity of a positive steady state of a metapopulation, x^*, where the dynamics are given by $(x(t)-x^*)' = A(x(t)-x^*)$ and A is no longer Metzler, then we need to extend our geometric interpretation of the ℓ_1 norm. In this case an equilibrium is reactive if the dot product of the derivative vector of any initial perturbation and the outward normal vector to the hypercube $|x_1 - x_1^*| + |x_2 - x_2^*| + \dots |x_n - x_n^*| = 1$ is positive. We could no longer use $\max_j \sum_{i=1}^n a_{ij} > 0$ to calculate reactivity, because $x(t) - x^*$ need not remain in the nonnegative cone. Thus an interesting area for future work would be to mathematically formulate reactivity in terms of the matrix A for positive equilibria of metapopulations.

No matter the norm in which reactivity and attenuation are measured, they are defined in terms of the linearization of a nonlinear system around an equilibrium. As mentioned in the introduction, reactivity and attenuation are therefore most relevant around hyperbolic equilibria, where the dynamics of the nonlinear system are well approximated by the linearized system. In section 3 we have shown that even in the linearized system it is possible for the population size to grow arbitrarily large before decaying or decay arbitrarily small before growing. In the latter case the zero equilibrium is unstable mathematically, but biologically the metapopulation could first go extinct if the total population size decays below one individual before it eventually increases.

It is also possible for an equilibrium of a nonlinear system to not be reactive, but for a perturbation of the nonlinear system to still cause a large excursion away from the stable equilibrium before eventually returning. Excitable systems, such as the FitzHugh–Nagumo system, have stable equilibria with attracting regions, but small perturbations still trigger large excitations [15, 38]. These systems may not be reactive from the linearized definition of reactivity, but can still exhibit similar behavior to reactivity in the nonlinear system, given a sufficient perturbation.

In this paper we use systems of differential equations to study reactivity, attenuation, and transients in birth-jump metapopulations. It may also be possible to study transients in metapopulations using methods by Wang, Efendiev, and Lutscher [56] for reaction-diffusion equations, where the spread of individuals between patches can be modelled mechanistically.

The final extension that we would like to highlight is the relationship between reactivity of continuous time models and reactivity of their discrete counterparts. Many marine metapopulations are modelled in discrete time due to yearly breeding cycles, but some are modelled in discrete time due to ease of simulation. For these models, where the time step is on the order of hours or days, we can connect the reactivity of the continuous time system with the discrete time system using a Taylor expansion. The continuous time system, $x' = Ax$, has the solution $x(t) = e^{At}x_0$ that could be sampled at discrete time steps τ to create the discrete time system $x(t+\tau) = Bx(t)$, where $B = e^{A\tau}$.

The continuous time system $x' = Ax$ is reactive in ℓ_1 if A has a positive column sum (Lemma 2.1). In discrete time the system $x(t+\tau) = Bx(t)$ is reactive in ℓ_1 if B has a column sum that is greater than 1 [52]. Assuming τ is a small time step, then we can approximate $B = e^{A\tau} = I + A\tau + O(\tau^2)$. Thus we can see that if the system is reactive in continuous time, i.e., there is a positive column sum of A, then we can find a sufficiently short time step τ such that the discrete time system is also reactive, i.e., there is a column sum of B greater than 1. However, for a predetermined time step τ, there are continuous time systems $x' = Ax$ that are reactive but for which their discrete counterparts $x(t+\tau) = e^{A\tau}x(t)$ are not reactive. One

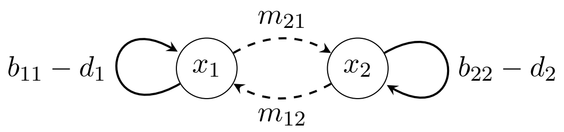


Figure 9. *Digraph for system (A.1). The directed edges represent the movement of individuals from the outgoing patch to the incoming patch. The self loops are the birth rate minus the death rate on a patch.*

such example is system (3.2) with $\epsilon = 0.9$ and $\tau = 1$.

Last, we hope our work can be used to better understand the transient dynamics in marine metapopulations for which habitat patches have already been classified as sources and sinks. For these systems the transient dynamics that may occur following a disturbance depend directly on the new distribution of the population. If the remaining population is distributed among sink patches, then it initially declines, even if it eventually recovers. Likewise if the population is distributed among source patches, then it initially grows, though this growth may not necessarily occur on the source patch itself. In addition, the relationship between transient dynamics and sources and sinks in marine metapopulations may also be useful when examining the dynamics that can occur following the protection of new marine environments, such as newly implemented Marine Protected Areas.

Appendix A. Two-patch example with migration.

Here we present an example of a two-patch metapopulation where individuals are born only onto their patch, but can now also migrate between patches. This is the case for many terrestrial species that live on patchy landscapes, where individuals can migrate between habitat patches. We present this example to demonstrate how Theorem 5.2 breaks down when V is not of the correct form. The dynamics of this metapopulation are described by the following set of ODEs:

$$\begin{aligned} x_1' &= b_1x_1 - m_{21}x_1 + m_{12}x_2 - d_1x_1, \\ x_2' &= b_2x_2 - m_{12}x_2 + m_{21}x_1 - d_2x_2, \end{aligned} \tag{A.1}$$

where b_i is the birth rate on patch i, m_{ij} is the migration rate from patch j to patch i, and d_i is the death rate on patch i. The lifecycle graph for this system is shown in Figure 9.

We again decompose $A = F - V$ and construct our next-generation matrix, $K = FV^{-1}$, though now V is not diagonal nor in the same form as required for Theorem 5.2.

$$\begin{aligned} A &= \begin{bmatrix} b_1 - m_{21} - d_1 & m_{12} \\ m_{21} & b_2 - m_{12} - d_2 \end{bmatrix}, \\ F &= \begin{bmatrix} b_1 & 0 \\ 0 & b_2 \end{bmatrix}, \\ V &= \begin{bmatrix} d_1 + m_{21} & -m_{12} \\ -m_{21} & d_2 + m_{12} \end{bmatrix}, \\ K = FV^{-1} &= \begin{bmatrix} \frac{b_1(d_2+m_{12})}{d_1d_2+d_1m_{12}+d_2m_{21}} & \frac{b_1m_{12}}{d_1d_2+d_1m_{12}+d_2m_{21}} \\ \frac{b_2m_{21}}{d_1d_2+d_1m_{12}+d_2m_{21}} & \frac{b_2(d_1+m_{21})}{d_1d_2+d_1m_{12}+d_2m_{21}} \end{bmatrix}. \end{aligned}$$

The entries of K may seem counterintuitive, but they represent the infinite sum of a geometric series. Consider the first entry, k_{11}. If we are tracking the total number of new individuals produced by one individual starting on patch 1, then this individual can either produce new offspring in patch 1 immediately, or it can migrate to patch 2, then back to patch 1 and produce offspring, or migrate again and produce more offspring. The entry k_{11} is then the birth rate in patch 1 multiplied by the residence time in patch 1, multiplied by a geometric series where the ratio is the probability of surviving the migration from patch 1 to patch 2 and then back to patch 1. Mathematically,

$$k_{11} = \frac{b_1}{m_{21} + d_1}\left[\sum_{i=0}^{\infty}\left(\frac{m_{21}}{m_{21} + d_1}\frac{m_{12}}{m_{12} + d_2}\right)^i\right].$$

Now consider λ_1 and R_1, the measures of transient growth for patch 1:

$$\begin{aligned} \lambda_1 &= b_1 - d_1, \\ R_1 &= \frac{b_1 d_2 + b_1 m_{12} + b_2 m_{21}}{d_1 d_2 + d_1 m_{12} + d_2 m_{21}}. \end{aligned}$$

We can see that

$$\lim_{d_2 \to \infty} R_1 = \frac{b_1}{d_1 + m_{21}}.$$

Therefore, even if $\lambda_1 > 0$, and so $b_1 > d_1$, as m_{21} becomes large, $R_1 < 1$.

In the other direction, if $d_1 = 2b_1$, then

$$\lim_{b_1 \to 0} R_1 = \frac{b_2}{d_2}.$$

Therefore, even if $R_1 > 1$, we can still have $\lambda_1 = b_1 - d_1 < 0$. We present this example to demonstrate that if the assumptions of Theorem 5.1 are not met, there is no longer a one-to-one relationship between λ_j and R_j.

Now we might also consider moving the off diagonal entries of V into F so that V becomes diagonal. This is similar to considering migrating individuals as new individuals entering a patch. In this case

$$\begin{aligned} F &= \begin{bmatrix} b_1 & m_{12} \\ m_{21} & b_2 \end{bmatrix}, \\ V &= \begin{bmatrix} d_1 + m_{21} & 0 \\ 0 & d_2 + m_{12} \end{bmatrix}, \\ K = FV^{-1} &= \begin{bmatrix} \frac{b_1}{d_1 + m_{21}} & \frac{m_{12}}{d_2 + m_{12}} \\ \frac{m_{21}}{d_1 + m_{21}} & \frac{b_2}{d_2 + m_{12}} \end{bmatrix}. \end{aligned}$$

Here $\lambda_1 = b_1 - d_1 > 0$ is equivalent to $b_1 > d_1$, which is then equivalent to $R_1 = (b_1 + m_{21})/(d_1 + m_{21}) > 1$. However, in this case R_1 no longer tracks the total number of new individuals produced on all patches over one generation. This new R_1 could perhaps be interpreted as the total number of new individuals produced on patch 1 by a single individual on patch 1 before that individual dies or migrates, plus the probability that the individual migrates to patch 2 before it dies. However, this will no longer be a biologically useful measure of a source or a sink.

Appendix B. Details for proof in subsection 3.1. Here we provide further details for the proof at the end of subsection 3.1 that follow after system (3.4). We want to show that

$$\lim_{\epsilon\to 0}\max_t\,(x(t)+y(t)) = \lim_{\epsilon\to 0}\rho_{\max} = \infty.$$

Normally to calculate the maximum we would take the derivative of $(x(t)+y(t))$, set it equal to 0, solve for t, and then evaluate $(x(t)+y(t))$ at this value of t. However, it turns out this is rather complicated, so we will simplify this process by first noting that $x(t)>0$ for all t. Therefore,

$$\max_t\,(x(t)+y(t)) > \max_t\, y(t).$$

Now we only have to perform the above process on $y(t)$, rather than $(x(t)+y(t))$.

Setting $y'(t)=0$ and solving for t, we find that the time that the maximum of $y(t)$ is achieved, $t_{\max}$, along with the corresponding maximum in y, $y(t_{\max})$, are

$$\begin{aligned} t_{\max} &= \frac{1}{\sqrt{2}}\left(\log(1+\sqrt{2})-\log(-1+\sqrt{2})\right),\\ y(t_{\max}) &= \frac{\sqrt{2}}{\epsilon}(1+\sqrt{2})^{\left(-\frac{1}{2}-\frac{1}{\sqrt{2}}\right)}(-1+\sqrt{2})^{\left(\frac{1}{\sqrt{2}}-\frac{1}{2}\right)}. \end{aligned}$$

We can clearly see that $\lim_{\epsilon\to 0} y(t_{\max})=\infty$ and thus also $\lim_{\epsilon\to 0}\max_t x(t)+y(t) = \lim_{\epsilon\to 0}\rho_{\max} = \infty$.

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