

RESEARCH ARTICLE

The structured demography of open populations in fluctuating environments

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Abstract

1. At the spatial scale relevant to many field studies and management policies, populations may experience more external recruitment than internal recruitment. These sources of recruitment, as well as local demography, are often subject to stochastic fluctuations in environmental conditions. Here, we introduce a class of stochastic models accounting for these complexities, provide analytic methods for understanding their long-term behaviour and illustrate the application of methods to two marine populations.
2. The population state $\mathbf{n}(x)$ of these stochastic models is a function or vector keeping track of densities of individuals with continuous (e.g. size) or discrete (e.g. age) traits x taking values in a compact metric space. This state variable is updated by a stochastic affine equation $\mathbf{n}_{t+1} = \mathbf{A}_{t+1}\mathbf{n}_t + \mathbf{b}_{t+1}$ where \mathbf{A}_{t+1} is a time varying operator (e.g. an integral operator or a matrix) that updates the local demography and \mathbf{b}_{t+1} is a time varying function or vector representing external recruitment.
3. When the realized per-capita growth rate of the local demography is negative, we show that all initial conditions converge to the same time-varying trajectory. Furthermore, when $\mathbf{A}_1, \mathbf{A}_2, \dots$ and $\mathbf{b}_1, \mathbf{b}_2, \dots$ are stationary sequences, this limiting behaviour is determined by a unique stationary distribution.
4. When the stationary sequences are periodic, uncorrelated or a mixture of these two types of stationarity, we derive explicit formulas for the mean, within-year covariance and autocovariance of the stationary distribution. Sensitivity formulas for these statistical features are also given.
5. The analytic methods are illustrated with applications to discrete size-structured models of space-limited coral populations and continuously size-structured models of giant clam populations.

KEYWORDS

covariance formulas, integral projection models, matrix models, open populations, sensitivity formulas, stationary distributions

1 | INTRODUCTION

Recruitment corresponds to the addition of juveniles to a population through either local births or immigration events. When recruitment mainly occurs through local births, the population is closed, else it is

open. At smaller spatial scales, which are often the scales at which empirical studies are conducted, open populations are common. This is especially common in species which only disperse during one life stage, such as plants with seed dispersal, insects with aerial dispersal and marine organisms with larval dispersal (Hixon, Pacala, &

Sandin, 2002). The simplest model of open populations are affine models, $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t + \mathbf{b}$, where \mathbf{n}_t is the population state at time t (e.g. a vector of population densities), \mathbf{A} describes the local demographic processes (e.g. a matrix accounting for survival, growth, reproduction and emigration) and \mathbf{b} describes external recruitment (Caswell, 2008; Pascual & Caswell, 1991; Roughgarden, Iwasa, & Baxter, 1985). If this population relies on external recruitment to persist (i.e. the dominant eigenvalue λ of \mathbf{A} is <1), the population approaches a steady state $\hat{\mathbf{n}} = (\mathbf{I}d - \mathbf{A})^{-1}\mathbf{b}$ that depends on the interactive effects of external recruitment and local demography. This reliance on external recruitment may be due to a population living in a sink habitat where death rates exceed birth rates (Dias, 1996; Pulliam, 1988) or may be due to most newly born individuals emigrating. In either case, models of this form have been used successfully to understand the dynamics of open sessile populations with space limited recruitment (Pascual & Caswell, 1991; Roughgarden et al., 1985; Svensson et al., 2004), age-structured reef fish populations (Armsworth, 2002), and coral and clam populations with continuous size structure (Madin, Hughes, & Connolly, 2012; Yau, Lenihan, & Kendall, 2014).

Open populations often experience environmentally driven fluctuations in external recruitment. If these fluctuations are serially uncorrelated and the population state is finite-dimensional (i.e. \mathbf{n}_t is a vector of densities), then one can model these populations by a first-order multivariate autoregressive, MAR(1), model: $\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t + \mathbf{b}_t$ (Bartlett, 1978; Cooper, Spencer, & Bruno, 2015; Gross & Edmunds, 2015; Ives, Dennis, Cottingham, & Carpenter, 2003; Reinsel, 2003). For these models, there is a unique stationary distribution provided that $\lambda < 1$, and explicit formulas for the mean and covariance matrix of this stationary distribution are well-known (Bartlett, 1978; Ives et al., 2003; Reinsel, 2003). More recently, Gross and Edmunds (2015) developed sensitivity formulas for these means and covariances.

These MAR(1) models, however, do not account for fluctuations in local demography (i.e. \mathbf{A} is time dependent), continuous population structure (e.g. size) or temporally correlated demographic fluctuations, although the importance of these population features is recognized. For example, Yau et al. (2014) used a continuous size-structured IPM to investigate how the degree of self-recruitment (used as a metric for the openness of the population) influenced management priorities of a giant clam fishery. Additionally, a series of matrix models was developed to account for space-limited recruitment in barnacle (Hyder, Aberg, Johnson, & Hawkins, 2001; Roughgarden et al., 1985) and coral (Pascual & Caswell, 1991) populations. As a result of how space-limited recruitment was incorporated into the model structure, the amount of settlement influenced both \mathbf{b} and \mathbf{A} . These models were extended by Svensson et al. (2004); Svensson, Jenkins, Hawkins and Åberg (2005) to investigate the relative importance of variability in recruitment, local survival and migration. The models also accounted for correlated fluctuations in demography, through the use of randomly selected winter/summer periodic transition matrices. However, no analytic methods have been developed that account for these three biological features.

To address these fundamental biological complexities, we develop results for analysing open population models accounting for (1) stationary and non-stationary fluctuations in local demography and recruitment, and (2) any mixture of continuous and discrete population structure. Our results include conditions ensuring convergence of the processes for stationary and non-stationary environments, formulas for mean and covariance structure of the stationary distributions of the processes for any mixture of periodic and serially uncorrelated fluctuations, and sensitivity formulas for these statistical features.

To highlight the broad applicability of our results, we apply them to a discrete size-structured model of space-limited coral populations (building off of the model of Pascual and Caswell (1991)), as well as a continuously size-structured model of giant clam populations (building off of the model of Yau et al. (2014)). Specifically, we demonstrate the use of our results to investigate the impact of the frequency of high recruitment years on the stationary distribution, the size-specific mean density and SD of the mean density and the correlation and autocorrelation structure across sizes. We also investigate the impact of the density of recruits during high and low recruitment years, as well as the degree of local retention, on these population properties. Finally, we assess the size-specific sensitivity and elasticity of the mean density and SD of the mean density to the probability of a high recruitment year and the density of recruits during a high recruitment year. In marine populations especially, these questions are of particular importance as recruitment is influenced by a wide range of potentially stochastic events (e.g. climate, physical processes, local demography and biological traits, etc.; Cowen and Sponaugle (2009)). Additionally, many of these populations are of conservation or economic interest, and so developing a framework to understand the interaction between stochastic events and population properties is essential.

2 | MODELS

Let S be the set of individual states for the population of interest. For example, for a stage-structured matrix model $S = \{1, 2, \dots, k\}$ where states may correspond to a finite number of stages, ages or spatial locations (Caswell, 2001). Alternatively, for the simplest integral projection models (IPMs) (Easterling, Ellner, & Dixon, 2000), $S = [a, b]$ corresponding to the continuum of sizes of individuals from the smallest of size a to the largest of size b . More generally, S may correspond to a mixture of continuous and discrete structure. For example, for a size and age-structured population, $S = [a, b] \times \{1, \dots, k\}$ where k is the maximal age of an individual (Ellner & Rees, 2006). A common feature of all these examples is that S is a compact metric space which we assume is the case for all the models discussed here.

To keep track of the densities of individuals, we have functions $\mathbf{n}: S \rightarrow [0, \infty)$ where $\mathbf{n}(x)$ is the “density” of individuals in state x . In general, we assume the functions \mathbf{n} are continuous functions, but more general classes of functions are allowed as discussed in the Appendices. Let $\mathbf{n}_t(x)$ denote the density of state x at time t .

To project the density function \mathbf{n}_t forward in time, we have contributions due to individuals in the population and contributions from outside of the population. To describe the endogenous contributions, let \mathbf{A}_{t+1} be a linear operator taking non-negative, continuous functions to non-negative, continuous functions. To describe the exogenous contributions, let $\mathbf{b}_{t+1}(x)$ be the density of individuals in state x entering the population externally at time $t + 1$. Then, the population model becomes

$$\mathbf{n}_{t+1} = \mathbf{A}_{t+1}\mathbf{n}_t + \mathbf{b}_{t+1}. \tag{1}$$

For a matrix model, \mathbf{A}_{t+1} is a $k \times k$ non-negative matrix, \mathbf{b}_{t+1} is a non-negative vector and $\mathbf{A}_{t+1}\mathbf{n}_t + \mathbf{b}_{t+1}$ corresponds to the usual matrix multiplication and vector addition. For the standard size-structured IPM, \mathbf{A}_{t+1} is an integral operator of the form

$$(\mathbf{A}_{t+1}\mathbf{n}_t)(x) = \int_a^b k_{t+1}(y,x)\mathbf{n}_t(y)dy + \mathbf{b}_{t+1}(x)$$

where $k_{t+1}(y,x)$ is a non-negative kernel describing the contribution of individuals of size y to individuals of size x at time $t + 1$ and \mathbf{b}_{t+1} is a continuous function from $[a,b]$ to $[0,\infty]$.

Given a population density function \mathbf{n} , let $\|\mathbf{n}\|$ be a norm corresponding to the total size of the population. For a matrix model, this norm is $\|\mathbf{n}\| = \sum_x \mathbf{n}(x)$. For the standard IPM, two choices of this norm are the L^1 norm $\|\mathbf{n}\| = \int_a^b \mathbf{n}(x)dx$ or the sup norm $\|\mathbf{n}\| = \sup_{x \in S} \mathbf{n}(x)$. These norms on \mathbf{n} also induces an operator norm on the operators \mathbf{A}_t given by

$$\|\mathbf{A}_t\| = \sup_{\|\mathbf{n}\|=1} \|\mathbf{A}_t\mathbf{n}\|.$$

In the case of the L^1 norm, this operator norm corresponds to the largest population size that can be achieved at time t for a population of size one at time $t - 1$ (i.e. $\|\mathbf{n}_{t-1}\| = 1$).

3 | RESULTS: GENERAL THEORY

We introduce three types of results. First, we present results for when the model converges to a time varying solution that is independent of initial conditions. Our condition for convergence applies to non-stationary as well as stationary environments. For stationary environments, this convergence is to a unique stationary distribution. Second, to understand the nature of these stationary distributions, we examine three special cases: periodic environments, temporally uncorrelated environments and uncorrelated fluctuations around a periodic environment. Finally, we derive sensitivity formulas for properties of the asymptotic behaviour in the three special cases.

3.1 | Convergence

Under mild assumptions, we introduce a natural condition that ensures the solutions of (1) converge to a time varying solution which is independent of the initial state of the system. The proof for this assertion

follows from an argument of Brandt (1986) who studied a one-dimensional version of (1) in uncorrelated environments. Iterating the model (1) forward from time 0 to time t yields the solution:

$$\mathbf{n}_t = \underbrace{\mathbf{A}_t\mathbf{A}_{t-1} \dots \mathbf{A}_1\mathbf{n}_0}_{=(\prod_{i=1}^t \mathbf{A}_i)\mathbf{n}_0} + \underbrace{\mathbf{A}_t\mathbf{A}_{t-1} \dots \mathbf{A}_2\mathbf{b}_1 + \mathbf{A}_t\mathbf{A}_{t-1} \dots \mathbf{A}_3\mathbf{b}_2 + \dots + \mathbf{A}_t\mathbf{b}_{t-1} + \mathbf{b}_t}_{=b_t + \sum_{\tau=2}^t (\prod_{i=\tau}^t \mathbf{A}_i)\mathbf{b}_{\tau-1}} \tag{2}$$

Importantly, only the first term depends on the initial state \mathbf{n}_0 of the population.

When this first term in (2) vanishes exponentially fast, we might expect that \mathbf{n}_t converges to a time varying solution which is independent of the initial condition. To make this statement precise, define the *realized per-capita growth rate* of the population as

$$r(\mathbf{A}_t) := \limsup_{t \rightarrow \infty} \frac{1}{t} \log \|\mathbf{A}_t\mathbf{A}_{t-1} \dots \mathbf{A}_1\|.$$

This term measures the maximal long-term per-capita growth rate of the population in the absence of immigration, that is $\mathbf{b}_t = 0$ for all t . If $r(\mathbf{A}_t) < 0$, then the population tends exponentially toward extinction in the absence of immigration. Namely, the population is a *sink population*. If $r(\mathbf{A}_t) > 0$, then the population asymptotically increases at an exponential rate $r(\mathbf{A}_t)$ and is a *source population*.

For source populations, key properties of long-term dynamics, such as the long-term population growth rate, stable-state distribution and reproductive values, are determined by the “immigration-free” dynamics $\mathbf{n}_{t+1} = \mathbf{A}_{t+1}\mathbf{n}_t$ for which classical results in stochastic demography apply (Tuljapurkar, 1990). Hence, our results focus on the case of sink populations and we assume that $r(\mathbf{A}_t) < 0$. Furthermore, we assume that $\sup_t \|\mathbf{b}_t\| < \infty$. Under these assumptions, we show in Appendix S1 that all population trajectories converge exponentially fast toward one another. That is, given two population trajectories \mathbf{n}_t and $\tilde{\mathbf{n}}_t$ corresponding to initial conditions \mathbf{n}_0 and $\tilde{\mathbf{n}}_0$,

$$\limsup_{t \rightarrow \infty} \frac{1}{t} \log \|\mathbf{n}_t - \tilde{\mathbf{n}}_t\| \leq r(\mathbf{A}_t) \tag{3}$$

In particular, all population trajectories asymptotically approach the trajectory corresponding to the zero initial condition $\mathbf{n}_0 = 0$:

$$\mathbf{n}_t = \mathbf{b}_t + \sum_{\tau=2}^t \left(\prod_{i=\tau}^t \mathbf{A}_i \right) \mathbf{b}_{\tau-1}.$$

From a computational point of view, this result implies that it suffices to run the model once for any initial condition to understand its long-term behaviour.

3.2 | Stationary environments

Assume that $\mathbf{A}_1, \mathbf{A}_2, \mathbf{A}_3, \dots$ are a stationary and ergodic sequence of non-negative operators, and $\mathbb{E}[\max\{\log \|\mathbf{A}_t\|, 0\}] < \infty$. Kingman (1973)'s subadditive ergodic theorem implies there exists an r (possibly $-\infty$) such that

$$\lim_{t \rightarrow \infty} \frac{1}{t} \log \|\mathbf{A}_t\mathbf{A}_{t-1} \dots \mathbf{A}_1\| = r$$

with probability one. In particular, the realized per-capita growth rate $r(\mathbf{A}_t)$ equals r with probability one. This realized per-capita growth rate r corresponds to what Tuljapurkar (1990) calls the stochastic growth rate $\log \lambda_s$ of the population in the absence of immigration. In the mathematical literature, this common r value is known as the dominant Lyapunov exponent of the random sequence of operators (Ruelle, 1982).

If $r < 0$, then equation 3 implies that with probability one trajectories experiencing the same sequences of environmental conditions \mathbf{A}_t and \mathbf{b}_t but possibly different initial conditions converge to one another exponentially fast. Furthermore, from the ensemble perspective, we show in Appendix S2 that \mathbf{n}_t converges exponentially fast to a unique stationary distribution provided that $\mathbb{E}[\log \|\mathbf{b}_t\|] < \infty$. To define this stationary distribution, a standard probabilistic construction allows one to uniquely extend \mathbf{A}_t and \mathbf{b}_t to the past (i.e. $\dots, \mathbf{A}_{-2}, \mathbf{A}_{-1}, \mathbf{A}_0, \mathbf{A}_1, \mathbf{A}_2, \dots$ and $\dots, \mathbf{b}_{-2}, \mathbf{b}_{-1}, \mathbf{b}_0, \mathbf{b}_1, \mathbf{b}_2, \dots$) such that they are stationary and ergodic. Then, the unique stationary distribution is given by

$$\hat{\mathbf{n}}_t = \mathbf{b}_t + \sum_{\tau=1}^{\infty} \left(\prod_{i=t-\tau}^{t-1} \mathbf{A}_i \right) \mathbf{b}_{t-\tau}.$$

In the case of environments that are uncorrelated (i.e. independent and identically distributed), periodic or a mixture of these types, we can say more about the stationary distribution.

3.2.1 | Uncorrelated environments

Assume that $\mathbf{A}_1, \mathbf{A}_2, \dots$ is an independent and identically distributed sequence of non-negative operators, and $\mathbf{b}_1, \mathbf{b}_2, \dots$ is an independent and identically distributed sequence of density functions. In this case, we can write down an explicit, easily computed expression for the first- and second-order moments of the stationary distribution. These expressions are extensions of well-know expressions when $\mathbf{A}_t = \mathbf{A}$ are constant in time and finite-dimensional (Bartlett, 1978). To introduce these expressions, define $\bar{\lambda}$ to be the dominant eigenvalue of $\bar{\mathbf{A}} := \mathbb{E}[\mathbf{A}_t]$ and $\bar{r} = \log \bar{\lambda}$. If $\bar{r} < 0$ and $\mathbb{E}[\|\mathbf{b}_t\|] < \infty$, then

$$\bar{\mathbf{n}} := \mathbb{E}[\hat{\mathbf{n}}] = (\text{Id} - \bar{\mathbf{A}})^{-1} \bar{\mathbf{b}}. \quad (4)$$

where $\bar{\mathbf{b}} = \mathbb{E}[\mathbf{b}_t]$ and Id denotes the identity operator: $\text{Id} \mathbf{n} = \mathbf{n}$ for all \mathbf{n} . As $\bar{r} > r$, the existence of the stationary distribution is not sufficient to ensure that its mean is well-defined. In fact, when $\bar{r} > 0 > r$, $\mathbb{E}[\|\hat{\mathbf{n}}\|]$ is infinite. We illustrate this phenomena with a simple scalar model in the examples section.

To define the covariance of $\hat{\mathbf{n}}$ for the general form of the model, we use tensor products of functions and linear operators. We briefly present the main definitions and refer the interested reader to (Hackbusch, 2012) for more details about tensor products on infinite-dimensional spaces and how to numerically approximate these tensor products. If f and g are functions from the individual state space S to the real numbers (e.g. two measurements associated with the state of an individual), then the tensor product $f \otimes g$ of f and g is a function from $S \times S$ to the real numbers that is defined by $(f \otimes g)(x, y) = f(x)g(y)$. When there are a finite number of individuals

states $S = \{1, 2, \dots, k\}$, $f \otimes g$ can be represented by a matrix whose i - j -th entry equals $(f \otimes g)(i, j) = f(i)g(j)$. The covariance of $\hat{\mathbf{n}}$, denoted by $\mathbf{Cov}[\hat{\mathbf{n}}]$, is given by $\mathbb{E}[(\hat{\mathbf{n}} - \bar{\mathbf{n}}) \otimes (\hat{\mathbf{n}} - \bar{\mathbf{n}})]$. When there are finite number of individual states $S = \{1, 2, \dots, k\}$, $\mathbf{Cov}[\hat{\mathbf{n}}](i, j)$ is the i - j -th entry of the covariance matrix of $\hat{\mathbf{n}}$.

In Appendix S3, we show that the covariance is well-defined when the spectral radius of $\mathbb{E}[\mathbf{A}_1 \otimes \mathbf{A}_1]$ is < 1 . Here, $\mathbf{A}_1 \otimes \mathbf{A}_1$ is the tensor product of \mathbf{A}_1 with itself. This tensor product is characterized by its action on elementary tensors $f \otimes g$ where f and g are functions from S to the reals for which $\mathbf{A}_1 f$ and $\mathbf{A}_1 g$ are well defined. Namely, $(\mathbf{A}_1 \otimes \mathbf{A}_1) f \otimes g = (\mathbf{A}_1 f) \otimes (\mathbf{A}_1 g)$ (Hackbusch, 2012). When this spectral radius of $\mathbb{E}[\mathbf{A}_1 \otimes \mathbf{A}_1]$ is < 1 , it is invertible and

$$\mathbf{Cov}[\hat{\mathbf{n}}] = (\text{Id} - \mathbb{E}[\mathbf{A}_1 \otimes \mathbf{A}_1])^{-1} \mathbf{Cov}[\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1]. \quad (5)$$

where $\mathbf{Cov}[K_1 \bar{\mathbf{n}} + \mathbf{b}_1] = \mathbb{E}[(\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1 - \bar{\mathbf{n}}) \otimes (\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1 - \bar{\mathbf{n}})]$ is the covariance operator of the single year fluctuations away from the mean population state. This covariance operator can be calculated directly using the distributional information about \mathbf{A}_1 and \mathbf{b}_1 (see e.g. Appendix S5 for calculations when \mathbf{A}_1 and \mathbf{b}_1 are drawn randomly from a finite set of operators and vectors, respectively).

In the finite-dimensional case, we can compute this covariance using the vec operation and the Kronecker product \otimes_K which corresponds to the tensor product in finite dimensions. Recall, for a $n \times n$ matrix A , the vec operation $\text{vec}(A)$ is a column vector of length n^2 given by concatenating the columns of A . For a $n \times n$ matrix A and $m \times m$ matrix B , the Kronecker product $A \otimes_K B$ is the $nm \times nm$ block matrix given by

$$A \otimes_K B = \begin{pmatrix} a_{11}B & a_{12}B & \dots & a_{1n}B \\ a_{21}B & a_{22}B & \dots & a_{2n}B \\ \vdots & \vdots & \dots & \vdots \\ a_{n1}B & a_{n2}B & \dots & a_{nn}B \end{pmatrix}.$$

In terms of these matrix operations, the covariance matrix is given by (Appendix S3)

$$\text{vec}(\mathbf{Cov}[\hat{\mathbf{n}}]) = (\text{Id} - \mathbb{E}[A \otimes_K A])^{-1} \text{vec}(\mathbf{Cov}[\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1]). \quad (6)$$

In the infinite-dimensional case, one can apply (6) to the finite-dimensional matrix approximations of \mathbf{A}_t and \mathbf{b}_t .

Even if \mathbf{A}_t and \mathbf{b}_t are uncorrelated in time, the population densities \mathbf{n}_t typically will exhibit temporal correlations whenever there are overlapping generations. To characterize these temporal correlations, the covariance between $\hat{\mathbf{n}}_t$ and $\hat{\mathbf{n}}_{t+\tau}$ equals

$$\mathbf{Cov}_\tau[\hat{\mathbf{n}}] = \mathbb{E}[(\hat{\mathbf{n}}_t - \bar{\mathbf{n}}) \otimes (\hat{\mathbf{n}}_{t+\tau} - \bar{\mathbf{n}})].$$

For $\tau \geq 1$, stationarity and independence imply

$$\mathbf{Cov}_\tau[\hat{\mathbf{n}}] = \mathbb{E} \left[(\hat{\mathbf{n}}_0 - \bar{\mathbf{n}}) \otimes \left(\prod_{i=\tau}^1 \mathbf{A}_i (\hat{\mathbf{n}}_0 - \bar{\mathbf{n}}) \right) \right]. \quad (7)$$

In finite dimensions, we can compute this autocovariance with the following equation:

$$\mathbf{Cov}_\tau[\hat{\mathbf{n}}] = \mathbf{Cov}[\hat{\mathbf{n}}] (\mathbf{A}^T)^\tau \quad (8)$$

where T denotes the matrix transpose. As $\mathbf{Cov}[\hat{\mathbf{n}}]$ is only well defined when $\bar{r} < 0$, (8) implies that the covariance terms, when they exist, decay exponentially fast with the length of the time lag τ .

Now assume that \mathbf{A}_t and \mathbf{b}_t depend on a parameter θ . Appendix S3 derives sensitivity formulas for the mean, the covariance and the autocovariance of the stationary distribution with respect to the parameter θ . The sensitivity of the mean $\bar{\mathbf{n}}$ of the stationary distribution $\hat{\mathbf{n}}_t$ is given by

$$\frac{\partial \bar{\mathbf{n}}}{\partial \theta} = (\mathbf{Id} - \bar{\mathbf{A}})^{-1} \left(\frac{\partial \bar{\mathbf{A}}}{\partial \theta} \bar{\mathbf{n}} + \frac{\partial \bar{\mathbf{b}}}{\partial \theta} \right). \quad (9)$$

This sensitivity formula is the same as what Caswell (2008) found for deterministic matrix models of the form $\bar{\mathbf{n}}_{t+1} = \bar{\mathbf{A}}\bar{\mathbf{n}}_t + \bar{\mathbf{b}}$. The sensitivity of $\mathbf{Cov}[\hat{\mathbf{n}}]$ to θ equals

$$\frac{\partial \mathbf{Cov}[\hat{\mathbf{n}}]}{\partial \theta} = (\mathbf{Id} - \mathbb{E}[\mathbf{A}_1 \otimes \mathbf{A}_1])^{-1} \left(\frac{\partial \mathbb{E}[\mathbf{A}_1 \otimes \mathbf{A}_1]}{\partial \theta} \mathbf{Cov}[\hat{\mathbf{n}}] + \frac{\partial \mathbf{Cov}[\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1]}{\partial \theta} \right). \quad (10)$$

In finite dimensions, we can compute these sensitivities with the vec and Kronecker product:

$$\text{vec} \left(\frac{\partial \mathbf{Cov}[\hat{\mathbf{n}}]}{\partial \theta} \right) = (\mathbf{Id} - \mathbb{E}[\mathbf{A}_1 \otimes_K \mathbf{A}_1])^{-1} \left(\frac{\partial \mathbb{E}[\mathbf{A}_1 \otimes_K \mathbf{A}_1]}{\partial \theta} \text{vec}(\mathbf{Cov}[\hat{\mathbf{n}}]) + \text{vec} \left(\frac{\partial \mathbf{Cov}[\mathbf{A}_1 \bar{\mathbf{n}} + \mathbf{b}_1]}{\partial \theta} \right) \right).$$

This finite-dimensional sensitivity formulas agrees with what Gross and Edmunds (2015) found for finite-dimensional MAR models where there is no variation in the \mathbf{A}_t matrices, that is $\mathbf{A}_t = \bar{\mathbf{A}}$ for all t . In this special case, $\mathbb{E}[\mathbf{A}_1 \otimes_K \mathbf{A}_1] = \bar{\mathbf{A}} \otimes_K \bar{\mathbf{A}}$. Finally, the sensitivity of the autocovariance for the finite-dimensional models equals

$$\frac{\partial \mathbf{Cov}_\tau[\hat{\mathbf{n}}]}{\partial \theta} = \frac{\partial \mathbf{Cov}[\hat{\mathbf{n}}]}{\partial \theta} (\bar{\mathbf{A}}^T)^\tau + \mathbf{Cov}[\hat{\mathbf{n}}] \sum_{i=0}^{\tau-1} (\bar{\mathbf{A}}^T)^{\tau-1-i} \frac{\partial \bar{\mathbf{A}}^T}{\partial \theta} (\bar{\mathbf{A}}^T)^i. \quad (11)$$

For the infinite-dimensional models, we apply this formula to their finite-dimensional discretization.

3.2.2 | Periodic environments

Consider a periodic environment with period T . Then, $\mathbf{A}_{t+T} = \mathbf{A}_t$ for all t . In the periodic environment, $r(\mathbf{A}_t)$ equals $\frac{1}{T} \log \lambda$ where λ is the dominant eigenvalue of the period T operator $\mathbf{A}_T \mathbf{A}_{T-1} \dots \mathbf{A}_2 \mathbf{A}_1$. In particular, the condition $r(\mathbf{A}_t) < 0$ corresponds to the dominant eigenvalue being < 1 . When this occurs, \mathbf{n}_t converges exponentially quickly to the periodic trajectory given by (Appendix S4)

$$\begin{aligned} \hat{\mathbf{n}}_0 &= (\mathbf{Id} - \tilde{\mathbf{A}})^{-1} \tilde{\mathbf{b}} \text{ and} \\ \hat{\mathbf{n}}_t &= \mathbf{A}_t \hat{\mathbf{n}}_{t-1} + \mathbf{b}_t \text{ for } 1 \leq t \leq T-1 \text{ where} \\ \tilde{\mathbf{A}} &= \prod_{i=T}^1 \mathbf{A}_i \text{ and } \tilde{\mathbf{b}} = \mathbf{b}_T + \sum_{\tau=2}^T \left(\prod_{i=T}^{\tau} \mathbf{A}_i \right) \mathbf{b}_{\tau-1} \end{aligned} \quad (12)$$

Now let θ be a parameter in the model. The sensitivity of the periodic solution, $\hat{\mathbf{n}}_0, \hat{\mathbf{n}}_1, \dots, \hat{\mathbf{n}}_{T-1}$, to θ is given by (Appendix S4)

$$\begin{aligned} \frac{\partial \hat{\mathbf{n}}_0}{\partial \theta} &= (\mathbf{Id} - \tilde{\mathbf{A}})^{-1} \left(\frac{\partial \tilde{\mathbf{A}}}{\partial \theta} \hat{\mathbf{n}}_0 + \frac{\partial \tilde{\mathbf{b}}}{\partial \theta} \right) \\ \frac{\partial \hat{\mathbf{n}}_t}{\partial \theta} &= \frac{\partial \mathbf{A}_t}{\partial \theta} \hat{\mathbf{n}}_{t-1} + \mathbf{A}_t \frac{\partial \hat{\mathbf{n}}_{t-1}}{\partial \theta} + \frac{\partial \mathbf{b}_t}{\partial \theta} \text{ for } t = 1, 2, \dots, T-1. \end{aligned}$$

3.2.3 | Uncorrelated fluctuations around a periodic signal

Stochastic variation in seasonal fluctuations or decadal oscillations can be modelled by combining the elements from the previous two examples. For descriptive purposes, assume there are T “seasons” per year and t counts the number of seasons that have elapsed. For each season, $1 \leq i \leq T$, let $\mathbf{A}_{i,0}, \mathbf{A}_{i,1}, \mathbf{A}_{i,2}, \dots$ and $\mathbf{b}_{i,0}, \mathbf{b}_{i,1}, \mathbf{b}_{i,2}, \dots$ be i.i.d. sequences. For any time, t , let $y(t) = [t/T] - 1$ correspond to the “year” and $s(t) = t - y(t)T$ the “season.” Then, we can write down a model of the following type:

$$\mathbf{n}_{t+1} = \mathbf{A}_{s(t+1), y(t+1)} \mathbf{n}_t + \mathbf{b}_{s(t+1), y(t+1)}. \quad (13)$$

The periodic “deterministic skeleton” of this model is given by $\mathbf{n}_{t+1} = \bar{\mathbf{A}}_{s(t+1)} \mathbf{n}_t + \bar{\mathbf{b}}_{s(t+1)}$ where $\bar{\mathbf{A}}_i = \mathbb{E}[\mathbf{A}_{i,t}]$ and $\bar{\mathbf{b}}_i = \mathbb{E}[\mathbf{b}_{i,t}]$.

To understand the first two moments of the stationary distribution, we can look at the “yearly stroboscope” version of the model:

$$\mathbf{n}_{kT+T} = \underbrace{\left(\prod_{i=T}^1 \mathbf{A}_{i,k} \right)}_{=: \mathbf{A}_{k+1}} \mathbf{n}_0 + \sum_{\tau=2}^T \underbrace{\left(\prod_{i=T}^{\tau} \mathbf{A}_{i,k} \right)}_{=: \mathbf{b}_{k+1}} \mathbf{b}_{\tau-1,k} + \mathbf{b}_{T,k} \quad (14)$$

As $\mathbf{A}_1, \mathbf{A}_2, \dots$ and $\mathbf{b}_1, \mathbf{b}_2, \dots$ as defined above are i.i.d. sequences, the results for the i.i.d. environments can be applied here.

4 | APPLICATIONS

To illustrate the applicability of the general methods, we apply them to a model of an unstructured population, a matrix model of reef corals (Hughes, 1984, Pascual & Caswell, 1991) and an integral projection model of giant clams (Yau et al., 2014). Schreiber and Moore (2018) provides the R code (R Core Team, 2016) for these examples and, more generally, code for implementing these methods to matrix and IPM models whose environmental dynamics are given by a finite state Markov chain.

4.1 | An unstructured, open population

The simplest stochastic, open model is for an unstructured population and takes the form

$$n_{t+1} = a_{t+1} n_t + b_{t+1}$$

where n_t , a_t and b_t are scalars. A continuous-time version of this model, for example, was used by Gonzalez and Holt (2002) to describe open, sink populations in a fluctuating environments. We assume that $a_t > 0$ and $b_t > 0$ are independent, identically distributed sequences. More specifically, $\log a_t$ and $\log b_t$ are normally distributed with means μ_a, μ_b , variances σ_a^2, σ_b^2 , and correlation ρ .

This model has a unique stationary distribution provided that $r = \mathbb{E}[\log a_t] = \mu_a < 0$ (Figure 1). The mean of this stationary distribution is finite if the arithmetic mean $\mathbb{E}[a_t]$ of a_t is < 1 . Namely,

$$\bar{a} = \mathbb{E}[a_t] = \exp(\mu_a + \sigma_a^2/2) < 1.$$

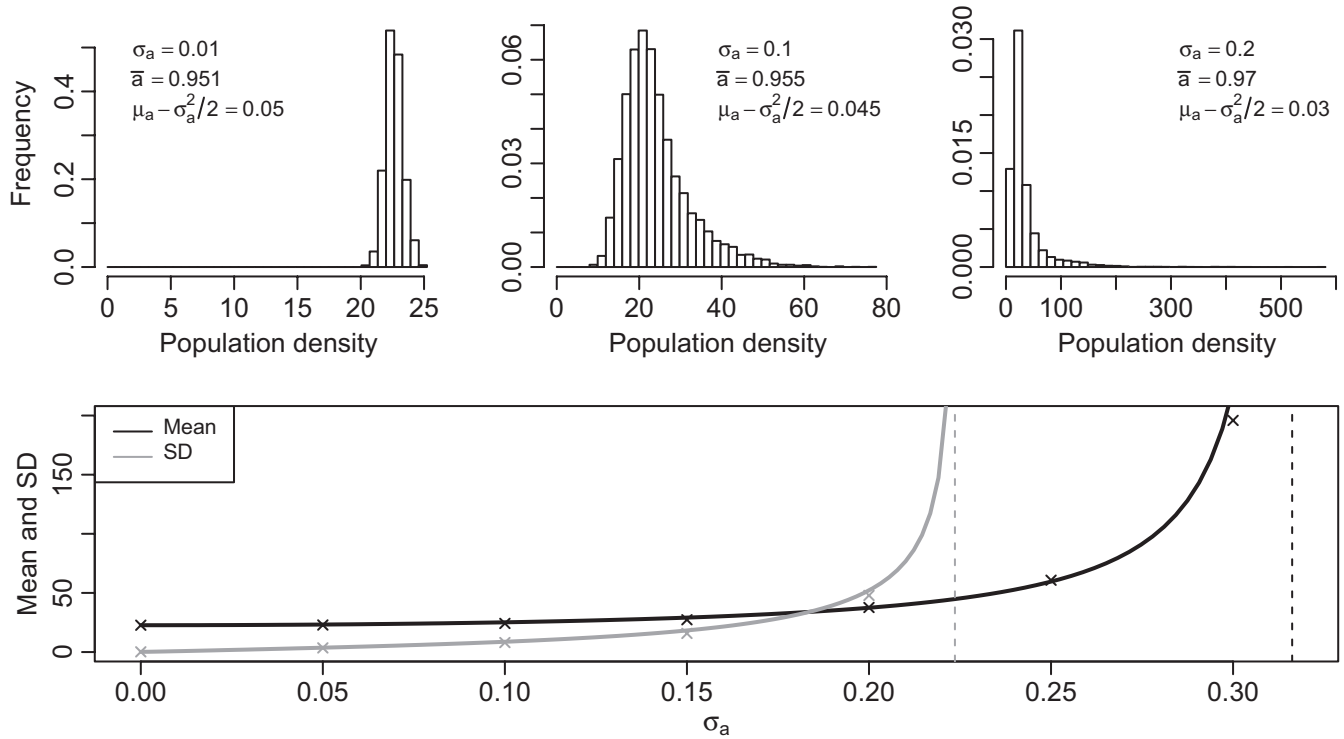


FIGURE 1 The effect of increasing within patch fluctuations σ_a on the mean and stationary distribution of the scalar model $n_{t+1} = a_{t+1}n_t + b_{t+1}$. In top panels, numerical approximations of stationary distributions for three levels of local fluctuations σ_a . In the bottom panel, the mean and SD of the stationary distribution as a function of σ_a . Solid line corresponds to the analytic formulas (15)–(16) and the crosses correspond to mean and SD of the numerically approximated stationary distribution. For the numerical approximations, the process was simulated for 100,000 years. Parameters: a_t is log-normally distributed with log mean $\mu_a = -0.05$ and standard deviation σ_a as shown. b_t is log-normally distributed with log mean $\mu_b = 0.05$ and log SD $\sigma_b = 0.05$. a_t and b_t are independent

Equivalently, $\mu_a < -\sigma_a^2/2$. As shown in the top panels of Figure 1, as $\sigma_a^2/2$ approaches μ_a , the stationary distribution becomes highly skewed with a “thick tail.” When it is well-defined, the mean of stationary distribution equals

$$\bar{n} = \frac{\bar{b}}{1 - \bar{a}} \quad (15)$$

where $\bar{b} = \mathbb{E}[b_t] = \exp(\mu_b + \sigma_b^2/2)$. This stationary distribution has a finite variance if

$$\mathbb{E}[a_t^2] = \exp(2\mu_a + 2\sigma_a^2) < 1.$$

Equivalently, $\mu_a < -\sigma_a^2$. Hence, \hat{n} has a finite mean but infinite variance whenever $-\sigma_a^2 < \mu_a < -\sigma_a^2/2$ (Figure 1). When the variance is finite, it equals

$$\text{Var}[\hat{n}] = \frac{\text{Var}[\beta_t]}{1 - \mathbb{E}[a_t^2]} \quad \text{where } \beta_t = a_t \bar{n} + b_t - \bar{n} \quad (16)$$

and

$$\begin{aligned} \text{Var}[\beta_t] &= \bar{n}^2 \text{Var}[a_t] + 2\bar{n} \text{Cov}[a_t, b_t] + \text{Var}[b_t] \\ &= \bar{n}^2 \exp(2\mu_a + \sigma_a^2) (\exp(\sigma_a^2) - 1) + 2\bar{n} \exp(\mu_a + \sigma_a^2/2) \\ &\quad \exp(\mu_b + \sigma_b^2/2) (\exp(\rho\sigma_a\sigma_b) - 1) \\ &\quad + \exp(2\mu_b + \sigma_b^2) (\exp(\sigma_b^2) - 1). \end{aligned}$$

As $\mathbb{E}[a_t^2] = \bar{a}^2 + \text{Var}[a_t]$, this expression for $\text{Var}[\hat{n}]$ implies that variation in the local dynamics ($\text{Var}[a_t \bar{n}]$) contributes more to the variation in the population densities ($\text{Var}[\hat{n}]$) than the variation in external recruitment ($\text{Var}[b_t]$) i.e. $\text{Var}[a_t]$ and $\text{Var}[b_t]$ appear in a symmetric manner in the numerator but the denominator decreases with $\text{Var}[a_t]$. Moreover, positive correlations between local dynamics and external recruitment increase the variance in the long-term population densities.

4.2 | Matrix model of reef corals with space-limited recruitment

We continue with a case study of an open population of reef corals with space-limited recruitment. Corals are sessile organisms with pelagic larvae. As such, recruitment is not strongly affected by local coral populations, but rather upon reproductive subsidies from external populations. Hughes (1984) first developed a size-structured, matrix population model of corals in a closed population. This model was extended by Pascual and Caswell (1991) to allow for open populations and space-limited recruitment. The model of Pascual and Caswell (1991) drew heavily upon the theoretical framework developed by Roughgarden et al. (1985) to describe open, age-structured barnacle populations with space-limited recruitment. We extend the model of Pascual and Caswell (1991) here to include stochastic recruitment.

Let $n_t(i)$ be the number of organisms in size class i at time t . At each time step, surviving individuals either remain in their current size class with probability $R(i)$ or grow to the next size class with probability $P(i)$. The average size, measured as an area, of each organism in a given size class is given by $a(i)$. New individuals enter the population at a rate proportional to the amount of free space available, where the settling parameter, s_{t+1} , is the number of larvae per unit area that enter the population and survive until the next census. If α is the total area of suitable substrate, then the amount of free, unoccupied substrate at each time step given by

$$\alpha - \sum_{i=0}^w a(i)n_t(i), \quad (17)$$

where w is the total number of size classes. The full model is then given by

$$\mathbf{n}_{t+1} = \mathbf{A}_{t+1}\mathbf{n}_t + \mathbf{b}_{t+1}, \quad (18)$$

with

$$\mathbf{A}_t = \begin{pmatrix} -s_t a(0) + R(0) & -s_t a(1) & -s_t a(2) & \dots & -s_t a(w) \\ P(0) & R(1) & 0 & \dots & 0 \\ 0 & P(1) & R(2) & \dots & 0 \\ \vdots & \vdots & \ddots & \ddots & 0 \\ 0 & \dots & \dots & P(w-1) & R(w) \end{pmatrix} \text{ and } \mathbf{b}_t = \begin{pmatrix} s_t \alpha \\ 0 \\ 0 \\ \vdots \\ 0 \end{pmatrix}. \quad (19)$$

To explore this model, we use the parameter values of Pascual and Caswell (1991) (adapted from Hughes (1984)). These parameter values were obtained from data for the reef coral *Agaricia agaricites* from 1978 to 1979. Corals were grouped into three size classes: 0–10 cm², 10–50 cm² and 50–200 cm². The total amount of available substrate is set equal to 12 m². With these choices, the matrix model becomes

$$\mathbf{A}_t = \begin{pmatrix} 0.5135 - 5s_t & -30s_t & -125s_t \\ 0.2072 & 0.6667 & 0 \\ 0 & 0.1746 & 0.7818 \end{pmatrix} \text{ and } \mathbf{b}_t = \begin{pmatrix} 120000s_t \\ 0 \\ 0 \end{pmatrix}. \quad (20)$$

We assume that settlement rates vary randomly between a low settlement rate of $s_\ell = 0.01$ and a high settlement rate of $s_h = 0.04$. These values lie below the critical settlement value of $s = 0.06$, above which the increased settlement rate leads to unstable and unbounded dynamics (Pascual & Caswell, 1991). Let p be the frequency of a high settlement year, with low settlement years occurring with frequency $1 - p$.

When the frequency of good years is low ($p = .05$), the stationary distribution is concentrated near the stable size distribution for the deterministic model with only bad years ($p = 0$; top panels in Figure 2). At intermediate frequencies of good years ($p = .5$), the stationary distribution becomes increasingly normally distributed from the smallest to largest size classes (bottom panels in Figure 2). The population exhibits the greatest mean densities when the frequency of good years is high (Figure 3a) and the greatest variation in abundances in all size classes when good years occur at an intermediate

frequency ($p \approx .4$ in Figure 3b). Intuitively, at high or low frequencies of good years, the dynamics are nearly deterministic and, consequently, exhibit minimal variation. Adjacent size classes exhibit weak, positive correlations in densities, while the largest and smallest size classes exhibit negative correlations (Figure 3c). As higher frequencies of good years leads to lower availability of substrate, these correlations are less positive or more negative at higher frequencies of good years. One year autocorrelations are greatest for the largest size class and least for the smallest size class (Figure 3d). Intuitively, stochastic recruitment only occurs in the smallest size class which reduces the correlation with densities in earlier years. Increasing frequency of good years make these stochastic recruitment events more consistent and, thereby, increase autocorrelations in the smallest size class.

To illustrate the use of the sensitivity and elasticity formulas, we examine elasticities of the mean and SD of density with respect to the densities of recruits arriving in good and bad years, that is s_h and s_ℓ . The details for computing the sensitivities and elasticities are presented in Appendix S5. The mean and SD in density is most sensitive to the density of recruits arriving in bad years, s_ℓ , particularly when the frequency of good years is low (Figure 4). Interestingly, the elasticity of mean densities is not stage-dependent. The elasticity of the SD is negative with respect to the density of recruits arriving in low recruitment years. The elasticity of the SD with respect to the density of recruits arriving in high recruitment years does depend slightly on stage, with smaller size classes showing a higher increase in SD with changes in s_h .

4.3 | Integral projection model of giant clam dynamics

In this example, we apply the above methods to a population of giant clams, *Tridacna maxima*, using data from Yau et al. (2014). Yau et al. (2014) developed two deterministic size-structured IPMs to describe a population of giant clams on Mo'orea, French Polynesia. One IPM assumed a completely closed population with no external recruitment, while the second IPM assumed a completely open population with no local retention. Yau et al. (2014) also investigated the amount of local retention that was required for the population to persist in the absence of external recruitment.

To parameterize the model, Yau et al. (2014) measured demographic rates of 1,949 clams annually from 2006 to 2010. Survival data was fit using nonlinear logistic regression, while growth data was fit using ordinary least squares regression of size at time $t + 1$ on size at time t . The variance in growth was also allowed to vary as a function of size. The size of new recruits was estimated using data on the size of clams <50 mm counted each year. Recruit size was assumed to be normally distributed with mean and SD estimated from the data. For the open model, the number of recruits was set equal to the average number of clams <50 mm that were counted each year. For the closed model, the number of recruits was assumed to be proportional to the size-specific adult gonadal mass, with only individuals >66.1 mm contributing reproductively to the population.

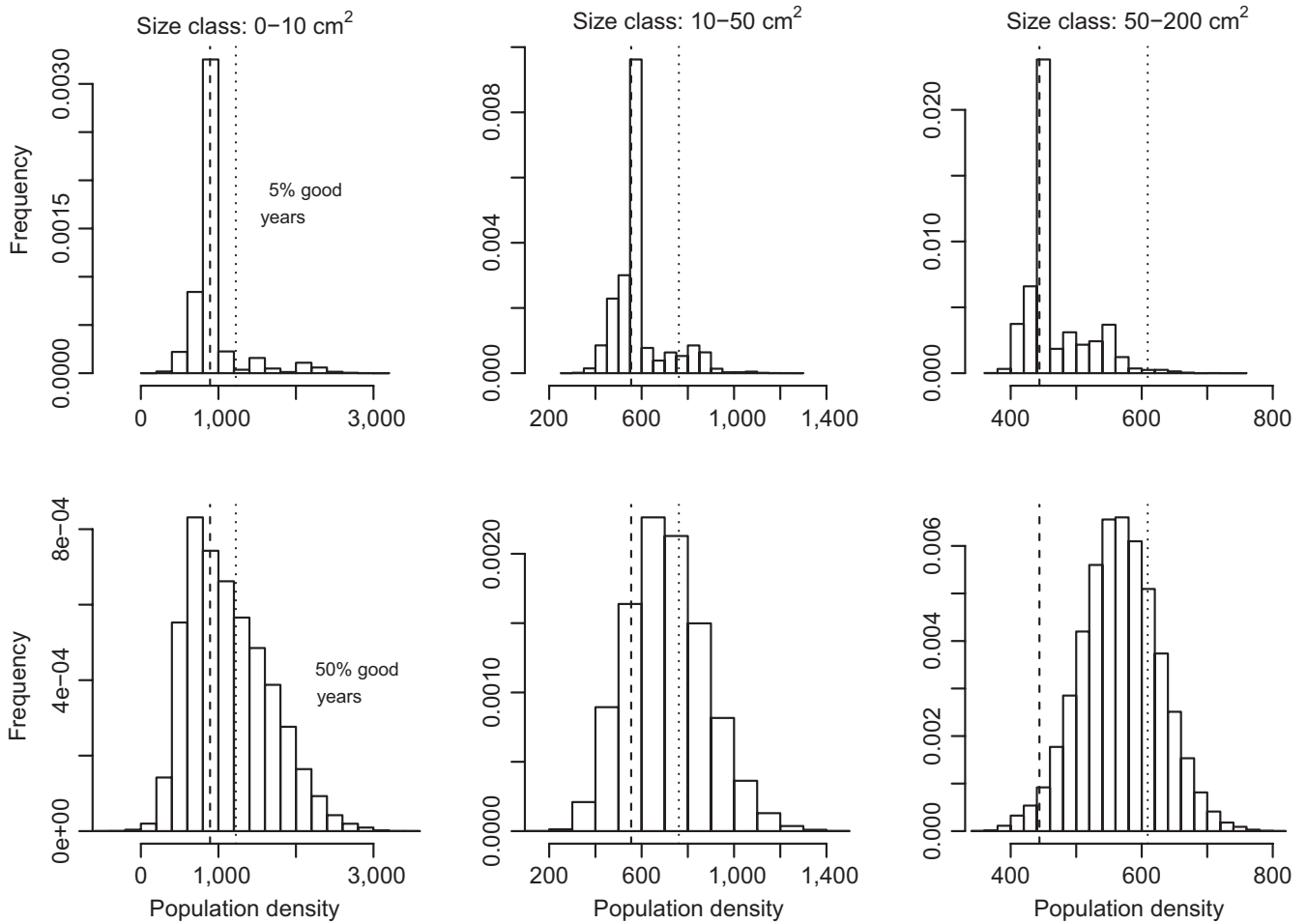


FIGURE 2 Numerical approximations of the stationary distribution, using a single long run of 100,000 years, for low frequencies ($p = .05$ in the top row) and intermediate frequencies ($p = .5$ in the bottom row) of good years. Columns corresponds to the different size classes. Dashed vertical lines indicate the population density for each size class with 0% good years ($p = 0$), while dotted vertical lines indicate the population density for each size class with 100% good years ($p = 1$). Parameters as described in the main text

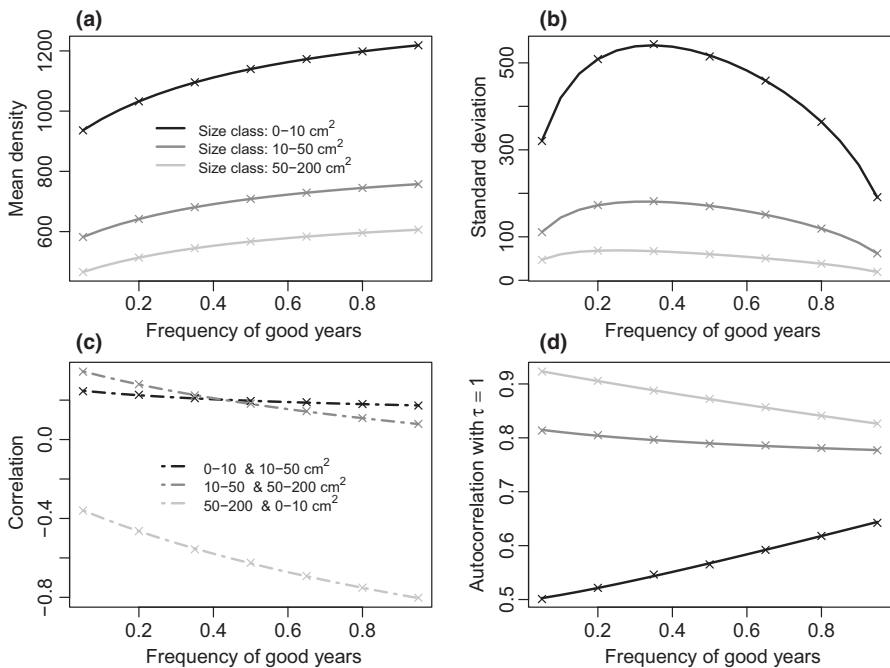


FIGURE 3 The effect of frequency of good years on mean density, standard deviations within size classes, correlations between size classes and temporal autocorrelation within size classes. Solid lines come from the analytic formulas and \times correspond to simulation estimates. Numerical simulations were run for 100,000 years. Parameters as described in the main text

FIGURE 4 The effect of the frequency of good years on the elasticity of the mean and standard deviation of coral densities with respect to the densities of recruits arriving in a good (solid line) and bad (dotted line) year. The only differences between stages occurs in the elasticity of the SD in good years. Parameters as described in the main text



Gonadal mass was converted to new recruits using a conversion factor, c_f , which was estimated by averaging the observed ratio of recruits to total gonadal mass each year. Finally, to determine the amount of local retention required for persistence, Yau et al. (2014) varied c_f to find the threshold such that the population transitioned from self-sustaining (population growth rate $\lambda > 1$) to declining ($\lambda < 1$). Table 1 shows the demographic functions and parameters used in the IPM.

For the stochastic IPM, we assume a population that includes both local retention and external recruitment. The model is written as

$$n(y,t+1) = \int_L^U (P(y,x) + F(y,x))n(x,t)dx + b(y,t+1)$$

where $P(y,x)$ represents the survival and growth of individuals from size x to size y , $F(y,x)$ represents the local recruitment and $b(y,t+1)$ represents the external recruitment. Clam sizes range from $L = 1$ to $U = 200$ mm. To incorporate stochasticity into the model, we generated four external recruitment vectors, one for each year of collected data: $\int b_1(x)dx = 84$, $\int b_2(x)dx = 167$, $\int b_3(x)dx = 178$ and $\int b_4(x)dx = 362$. Each b vector is assumed to occur with equal probability. Additionally, we varied the degree of local retention, c_f , from $c_f = 0$ (a fully open population with no local retention) to $c_f = 0.78$ (a population with λ just below 1 in the absence of external recruitment).

TABLE 1 Demographic functions and parameters used in the IPM, from Yau et al. (2014). The variable x represents the size of a clam, in mm. The parameter c_f is a conversion factor that converts grams of dry gonad mass to new recruits, and provides an indication of the degree of local retention, with $c_f = 0$ indicating no local retention

Functions	Equation
Survival	$\log\left(\frac{s(x)}{1-s(x)}\right) = 1.29 - \frac{19.14}{x+3.86}$
Growth	$g(x,y) = 21.15 + 0.869x$
Variance in growth	$\text{Var}(y) = 68.45 - 0.275x$
Recruit size	Normal with $\mu = 28.3$ and $\sigma^2 = 10.6$
Closed model	$f(x) = 5.64 \times 10^{-8} c_f x^{3.63}$
Fecundity	
Open model	84, 167, 178, 362
External recruitment	

Figure 5 shows the size-specific mean density, coefficient of variation and correlation between size at time t and size at time $t + 1$ for $c_f = 0$ (top panel) and $c_f = 0.7389$ (middle panel). While the size distribution remains roughly the same for different levels of c_f , overall more clams are present when local retention is higher. As expected, the coefficient of variation is highest for the smallest sized individuals that receive the greatest amount of stochastic external recruitment. Additionally, as c_f increases and the deterministic portion of the model becomes greater, the correlation across all sizes also increases, as expected.

We also investigated how the expected clam biomass, B , changes as a function of local retention. The expected total biomass of the population is equal to $\mathbb{E}[B] = \int_0^\infty w(x)\mathbb{E}[\hat{n}(x)]$, where $w(x)$ is a scaling parameter that converts an individual of size x to its biomass. The variance of the biomass is equal to $\text{var}[B] = \int \int w(x)w(y)\text{Cov}[\hat{n}(x),\hat{n}(y)]dxdy$. The bottom panel of Figure 5 shows the log of the expected biomass across the range of c_f values, as well as the log of the SD. As expected, as the degree of local retention increases such that the closed population growth rate λ nears 1, the log biomass increases substantially. Additionally, the variance in biomass decreases as c_f increases.

We examined the sensitivity of the mean density and the SD of the mean density to the probability of a particular recruitment year (Figure 6). We assume that if the probability of type i year, p_i , is increased by θ , then the probability of the remaining three year types is decreased by $\theta/3$. The details for computing these sensitivities are presented in Appendix S5. Our computations reveal that the mean density for all sizes is most sensitive to the frequency of the highest recruitment years and slightly less sensitive to the frequency of the lowest recruitment years (darkest versus lightest curves in the left panel of Figure 6). Mean densities are much less sensitive to the frequency of the intermediate recruitment years. In contrast, the SD of the densities in all sizes are least sensitive to the frequency of the lowest recruitment years and much more sensitive to frequencies of all the other types of recruitment years (lightest curve vs. all other curves in the right-hand panel of Figure 6). In all cases, the sensitivities follow the size distribution of the population.

5 | DISCUSSION

Here, we develop methods for analysing affine models of open populations with continuous and discrete population structure

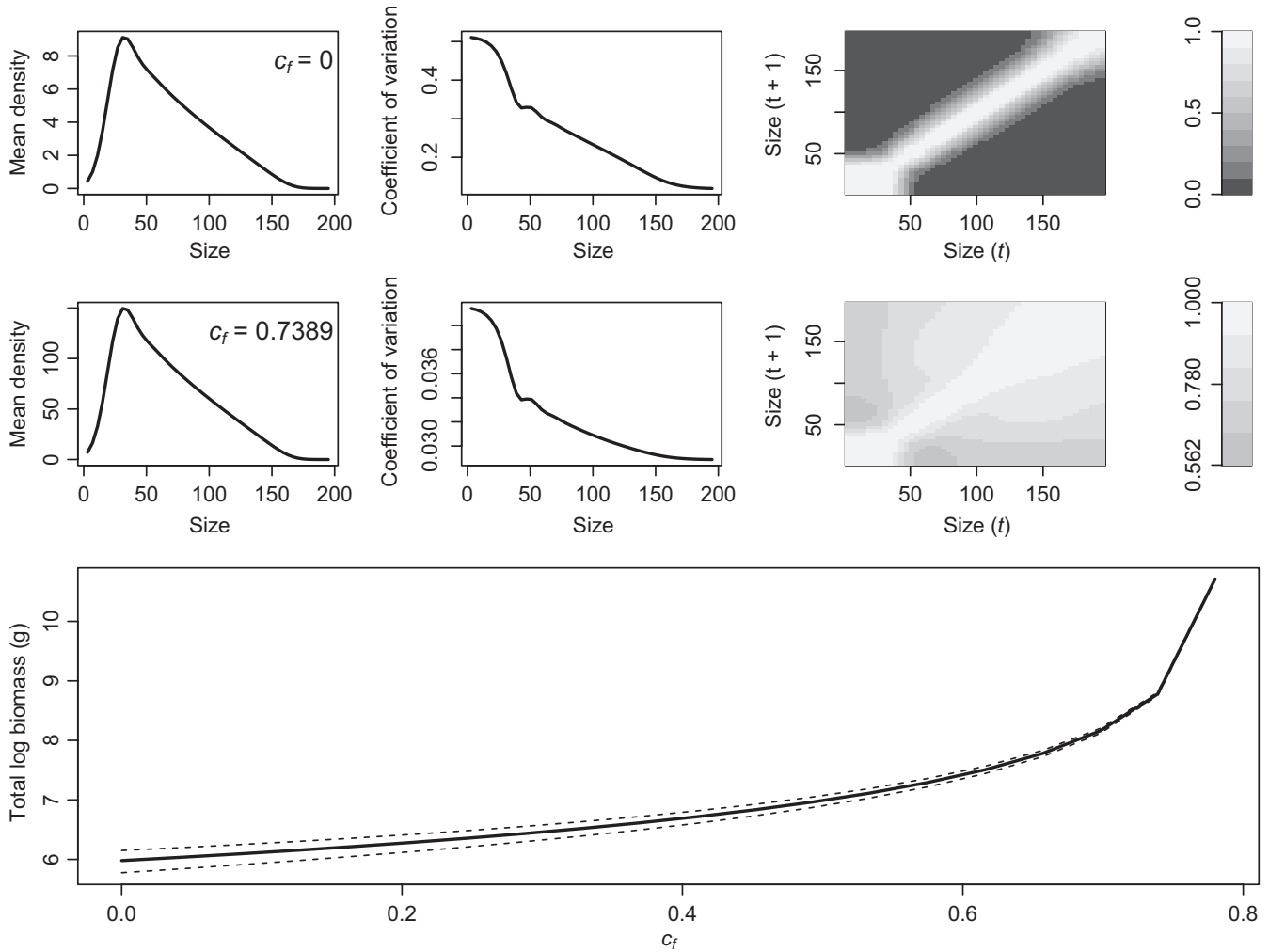


FIGURE 5 The size-specific mean density, coefficient of variation, and correlation between size at time t and size at time $t + 1$ in an open population with no local retention ($c_f = 0$; top panel), and a clam population with λ just below 1 in the absence of external recruitment ($c_f = 0.7389$; middle panel). The bottom panel shows the total log clam biomass as a function of the degree of local retention, c_f

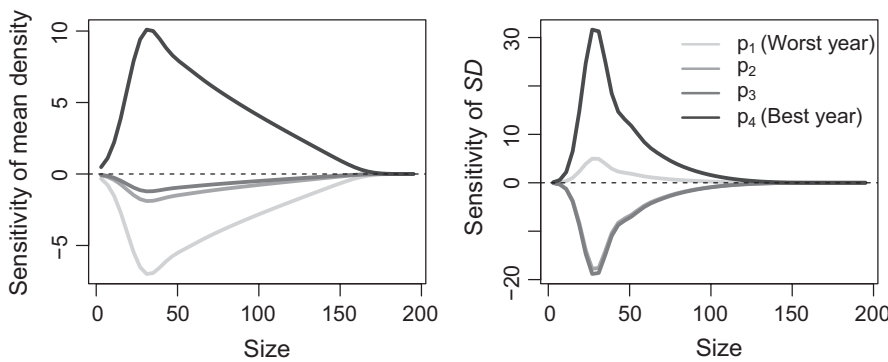


FIGURE 6 The sensitivity of the mean density and the SD of the mean density to changes in the frequency of a particular year, p_i , with p_1 representing the frequency of the worst year and p_4 representing the frequency of the best year. We assume that if the probability of type i year is increased by θ , then the probability of the remaining three year types is decreased by $\theta/3$

(e.g. size and stage) experiencing stochastic local demography and stochastic external recruitment. Provided that the local demography is unable to support the population (i.e. the local asymptotic growth rate is negative due to mortality and emigration exceeding reproduction), we show that all initial population states converge to the same asymptotic behaviour. When the environmental fluctuations are non-stationary, this limiting behaviour corresponds to a

“pull-back attractor” in the mathematical theory of non-autonomous systems (Kloeden & Rasmussen, 2011) which more recently has been dubbed an “asymptotically environmentally dependent trajectory” by Chesson (2017). When the environmental fluctuations are stationary, these limiting behaviours are characterized by a unique stationary distribution of the model. For environments with a mixture of periodic and serially uncorrelated fluctuations, we derived

explicit formulas for the mean and covariance of these stationary distributions and provide sensitivity formulas for these quantities. In particular, our results extend the work of (Gross and Edmunds, 2015) for discretely structured populations experiencing uncorrelated environments in only external recruitment.

We show, using a general, unstructured model, that variation in local dynamics contributes more to variance in population densities relative to variance in external recruitment. We show also that positive correlations between local dynamics and external recruitment increase the variance in long-term population densities, while negative correlations will decrease this variance. Finally, we show that, under certain conditions, it is possible for a population to be regulated, but have an infinite mean density. This effect occurs when the stochastic growth rate of the closed portion of the model is negative, but the log eigenvalue of the averaged system is positive. In this case, large, rare fluctuations contribute to the mean, but since the stochastic growth rate of the closed portion of the model is negative, the population remains regulated. This result provides an open population parallel to what Lewontin and Cohen (1969) found for closed populations: “even though the expectation of the population size may grow infinitely large with time, the probability of extinction may approach unity, owing to the difference between the geometric and arithmetic mean growth rates.”

We also show the application of the methods to two structured marine populations, specifically investigating the impact of changing the frequency of good recruitment years and changing the degree of openness of the population. In general, our results are intuitive. Mean population densities are highest when there is less variability in recruitment, while the *SD* of the mean population density is highest when there is greater variability in recruitment. With the IPM, we find that increases in mean density only occur with increasing the frequency of the best recruitment year, and that this effect is slightly greater than the negative effect of increasing the frequency of the worst recruitment year, likely due to relative distance of the best and worst recruitment levels from the average recruitment value. Moreover, using the matrix model, we find that a small number of good years is nearly as effective as a large number of good years at contributing to increases in mean densities, due to the dependence of recruitment on available open space.

Of particular interest is the use of the methods to study the covariance structure of the population. Using the IPM, we see that decreasing recruit variability by decreasing the degree of population openness leads to higher correlations across sizes of individuals in the population. Conversely, when recruit variability is high, correlation across sizes is reduced and is mostly through direct growth from one size to another between time steps. In the matrix model, correlation between sizes is positive for adjacent size classes (i.e. high population densities in one size class will lead to high densities in the next size class). However, the correlation between the smallest and largest size class is negative, with the relationship most negative when the frequency of good years is high. This is most likely due to the impact of space-limitation on recruitment. Finally, we can use the

methods to investigate the autocorrelation structure of the population between different time steps. For a single-year time step in the matrix model, we see that the autocorrelation is highest for the largest size classes (with no variable input) and lowest for the smallest size class (due to the variability in recruitment). As the frequency of good years increases, the autocorrelation of the smallest size class increases substantially.

While we used the methods presented here for models of open populations, they also apply to two other classes of models. First, consider a nonlinear, stochastic difference equation $\mathbf{n}_{t+1} = F(\mathbf{n}_t, \xi_t)$ where ξ_t describe the environmental fluctuations. If these fluctuations are “small” and $\hat{\mathbf{n}}$ is a stable equilibrium of the difference equation $\mathbf{n}_{t+1} = F(\mathbf{n}_t, 0)$, then the stochastic dynamics near this equilibrium may be approximated by $\mathbf{n}_{t+1} = \partial_{\mathbf{n}} F(\hat{\mathbf{n}}, 0)(\mathbf{n}_t - \hat{\mathbf{n}}) + \partial_{\xi} F(\hat{\mathbf{n}}, 0)\xi_t$ which is a model of the form considered here. Hence, our methods provide a means to approximate the covariance matrix of this linear approximation whenever the ξ_t are serially uncorrelated. Second, our methods also apply to extensions of multispecies models studied by (Cooper et al., 2015, Gross and Edmunds, 2015 and Ives et al., 2003). If x_i denotes the density of species i , these models take the form $x_i(t+1) = r_i(t)x_1(t)^{a_{i1}(t)}x_2(t)^{a_{i2}(t)} \dots x_n(t)^{a_{in}(t)}$ where $r_i(t)$ corresponds to intrinsic growth rates of species i and $a_{ij}(t)$ describes time-dependent species interactions. Setting $n_i = \log x_i$ yields a model of the form $\mathbf{n}_{t+1} = \mathbf{A}_t \mathbf{n}_t + \mathbf{b}_t$ where $\mathbf{A}_t = a_{ij}(t)$ and $\mathbf{b}_t = \log r_i(t)$. Hence, our results apply and generalize the work of (Cooper et al., 2015, Gross and Edmunds, 2015 and Ives et al., 2003) who assumed that the interaction terms did not vary in time.

In conclusion, when studying real-world populations, it is important to understand the interplay of open recruitment, stochasticity in demographic rates and population structure. This is particularly important when studying organisms with ecological, economic or public interest importance, such as invasive or threatened species, and when studying the effect of changing environmental conditions (e.g. due to climate change). Our results show that, for open populations, it is important to understand the effects of local demographic stochasticity, rather than focusing solely on variability in recruitment, as is often done, particularly for marine organisms. We also show that our methods can be used to directly assess the impact of decreases in the frequency of good years, as well as investigate the correlation between population states and changes in population states due to changing environmental conditions.

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AUTHORS' CONTRIBUTIONS

S.J.S. conceived the study with input from J.L.M. S.J.S. conducted the mathematical analysis and wrote the single variable example code. J.L.M. wrote the coral matrix and clam IPM code. S.J.S. and J.L.M. wrote the article.

DATA ACCESSIBILITY

All the data and R code used for the numerical examples are available at the Zenodo repository: <https://doi.org/10.5281/zenodo.1184176> (Schreiber & Moore, 2018).

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SUPPORTING INFORMATION

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