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A NOTE ON THE GLOBAL BEHAVIOR OF A NONLINEAR SYSTEM OF DIFFERENCE EQUATIONS

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ABSTRACT. This paper deals with the global asymptotic stability character of solutions of a discrete time deterministic model proposed by Wikan and Eide in Bulletin of Mathematical Biology, 66, 2004, 1685-1704. A stochastic extension of this model is proposed and discussed. Computer simulations suggest that the dynamics of the stochastic model includes a mixture of the dynamics observed in the deterministic model.

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1. INTRODUCTION

In their paper, Wikan and Eide [18] introduced a two stage discrete population model of the form

$$(1.1)\qquad \begin{cases} x_{n+1} = Fe^{-\beta_1 y_n} y_n + (1-\mu_1)e^{-\beta_2 y_n} x_n \\ \\ y_{n+1} = Pe^{-\beta_3 y_n} x_n + (1-\mu_2) y_n \end{cases} \qquad n = 0, 1, \dots,$$

The above model is an attempt to explain the oscillatory behavior observed in several fish populations, particularly in the North Atlantic cod stock.

The variables x_n and y_n represent the immature and respectively the mature populations at time n. The parameters β_1, β_2 and β_3 are referred to as cannibalism parameters. μ_1 and μ_2 are the natural death rates caused by factors other than cannibalism. Parameters F and P are the fecundity and respectively the survival rate from the immature to mature stage. Therefore, one has that $0 < P \leq 1$, $F > 0$, $0 < \mu_1 < 1$ and $0 < \mu_2 < 1$. Using data on fishing mortalities and biomasses, Wikan and Eide [18] estimated the parameters of the model (1.1). They showed that, for North Atlantic Cod, the least squares estimates for β_2 and β_3 were both zero, indicating that only cannibalism of immature cod by mature cod was supported by the data. This was further supported by empirical observation. Thus, throughout the current paper we consider that β_1 assumes a positive value, while $\beta_2 = \beta_3 = 0$.

As documented in Wikan and Eide ([18]), traditional stock recruitment models for fish stock assessment are based on specializations of the Deriso [10] and Schnute [16] recruitment function f, where

$$f(x) = F\left(1 - \gamma\beta x\right)^{\frac{1}{\gamma}}$$

(see, for example, Lassen and Medley [14] for further discussion on model development and estimation). The work of Wikan and Eide focus on the Ricker specialization (where $\gamma \to 0$) (Ricker [15]). They also mention the Beverton and Holt specialization (where $\gamma = -1$) (Beverton and Holt [3]) in the last paragraph of their paper. In each of these particular cases, local stability analysis was performed. While global stability analysis was left out, we believe that describing the regions of global asymptotic stability (even in special cases of interest) will complement the results in Wikan and Eide ([18]).

A model that incorporates both relations, Ricker and Beverton-Holt, and the already estimated cannibalism parameters is as follows:

$$(1.2)\qquad \begin{cases} x_{n+1} = Fh(y_n) y_n + (1-\mu_1) x_n \\ \\ y_{n+1} = P x_n + (1-\mu_2) y_n \end{cases} \qquad n = 0, 1, \dots$$

where the function h can be specialized to: (i) exponential form, $h(y) = e^{-\beta_1 y}$ (Ricker) and (ii) rational form, $h(y) = 1/(1 + \beta_1 y)$ (Beverton-Holt). In both cases, h is a strictly monotone decreasing function.

The goal of this paper is two fold. We address the global asymptotic behavior of solutions of system (1.2). A complete description is given especially for the case when the function h is of rational Beverton-Holt type.

We also investigate the impact of uncertainty due to influences from environmental changes, ecosystem dynamics and changes in fishing patterns by allowing certain parameters within (1.2) to be random. While Wikan and Eide [18] suggest that such factors could help explain observed fluctuations in fish stock biomass, they do not attempt to incorporate them in their analysis. Using a stochastic model and simulations we explore the possible influences of such uncertainty on the equilibrium solution and resulting limiting system dynamics. The behavior of trajectories of nonlinear deterministic and stochastic discrete time systems arising in ecology and biology has been the focus of many research studies (Cushing el al. [5] and [6], S.M. Henson et al. [9], Dennis et al. [7], Kesinger and Allen [12]).

The paper is organized as follows. Sections 2 and 3 deal with the existence of equilibrium points and the boundedness of solutions. Section 4 deals with the local and global stability of equilibrium points. Section 5 demonstrates the impact of random model parameters on the nature of the equilibrium solution and the resulting system behavior. The paper ends with conclusions.

2. EQUILIBRIUM POINTS

The equilibrium points are solutions of the following system of equations

$$\left\{ \begin{array}{l} \bar{x} = Fh(\bar{y})\bar{y} + (1-\mu_1)\bar{x} \\ \bar{y} = P\bar{x} + (1-\mu_2)\bar{y} \end{array} \right. \tag{2.1}$$

Combining the equations we have $\bar{y} = \dfrac{PF}{\mu_1\mu_2}h(\bar{y})\bar{y}$. Thus, $(0,0)$ is always an equilibrium. In the case $\bar{y} \neq 0$, then

$$\bar{y} = h^{-1}(\frac{\mu_1\mu_2}{PF}) \quad \text{and} \quad \bar{x} = \frac{\mu_2}{P}h^{-1}(\frac{\mu_1\mu_2}{PF}).$$

Let us note that the positive equilibrium exists if $h^{-1}(\frac{\mu_1\mu_2}{PF}) > 0$. Applying h yields $h(h^{-1}(\frac{\mu_1\mu_2}{PF})) < h(0) = 1$ or equivalently $\mu_1\mu_2/PF < 1$. Denote

$$R_0 = PF/\mu_1\mu_2.$$

PF represents the growth (birth) rate of the population, while the $\mu_1\mu_2$ represents the death rate of the population. Mathematically, if $R_0 = PF/\mu_1\mu_2 \leq 1$ then $(0,0)$ is the only equilibrium point. If $R_0 = PF/\mu_1\mu_2 > 1$ then system (1.2) has two equilibria, namely $E_1(0,0)$ and $E_2(\bar{x},\bar{y})$, where $\bar{y}$ is as in the table below and $\bar{x} = \dfrac{\mu_2}{P}\bar{y}$.

Ricker	Beverton-Holt
$h(y) = e^{-\beta_1 y}$	$h(y) = \dfrac{1}{1+\beta_1 y}$
$h^{-1}(y) = -\dfrac{1}{\beta_1}\ln y$	$h^{-1}(y) = \dfrac{1-y}{\beta_1 y}$
$\bar{y} = \dfrac{1}{\beta_1}\ln(\dfrac{PF}{\mu_1\mu_2})$	$\bar{y} = \dfrac{1}{\beta_1}(\dfrac{PF}{\mu_1\mu_2} - 1)$

In the sequel, our analysis deals with analytical results concerning the behavior of solutions of system (1.2) in all three cases of interest: (i) $R_0 < 1$, (ii) $R_0 = 1$ and (iii) $R_0 > 1$.

3. BOUNDEDNESS OF SOLUTIONS

In this section we prove that the solution gets trapped in an invariant box. Obviously, for $y \geq 0$ we have

$$ye^{-\beta_1 y} \leq 1/(\beta_1 e) < 1/\beta_1$$

and

$$y/(1+\beta_1 y) \leq 1/\beta_1.$$

Let

$$M = 1/\beta_1$$

be the bound for both functions of the form $yh(y)$. We now give the following lemma which demonstrates the boundedness of solutions of the system (1.2).

Lemma 3.1. *Let* $\{(x_n, y_n)\}_{n\geq 0}$ *be a non-negative solution of system* (1.2).

i) *The compact set* $[0, (FM)/\mu_1] \times [0, (PFM)/\mu_1\mu_2]$ *is invariant.*
ii) *In particular,* $\limsup_{n\to\infty} x_n \leq (FM)/\mu_1$ *and* $\limsup_{n\to\infty} y_n \leq (PFM)/\mu_1\mu_2$.

Proof. We show invariance first. Take (x_N, y_N) in $[0, (FM)/\mu_1] \times [0, (PFM)/\mu_1\mu_2]$, for some N. Then

$$\begin{aligned} x_{N+1} &= Fh(y_N)y_N + (1-\mu_1)x_N && \text{first equation in (1.2)} \\ &\leq FM + (1-\mu_1)x_N \\ &\leq FM + (1-\mu_1)\frac{FM}{\mu_1} = \frac{FM}{\mu_1} \end{aligned}$$

From the second equation, $y_{N+1} = Px_N + (1-\mu_2)y_N$. We have

$$y_{N+1} = Px_N + (1-\mu_2)y_N \leq P\frac{FM}{\mu_1} + (1-\mu_2)\frac{PFM}{\mu_1\mu_2} = \frac{PFM}{\mu_1\mu_2}.$$

Thus the set is invariant. Since $yh(y)$ has a maximum value, using the first equation of (1.2)

$$x_{n+1} \leq FM + (1-\mu_1)x_n$$

Using that $1-\mu_1 < 1$ it is obvious that $\limsup_{n\to\infty} x_n \leq \dfrac{FM}{\mu_1}$. From the second equation in (1.2), we obtain that for every $\varepsilon > 0$, there is some $N_\varepsilon \geq 0$ such that $y_{n+1} \leq \dfrac{PFM}{\mu_1} + (1-\mu_2)y_n + \varepsilon$ for all $n \geq N_\varepsilon$.

But $\varepsilon > 0$ is arbitrary and $0 < \mu_2 < 1$ and thus

$$\limsup_{n\to\infty} y_n \leq \frac{PFM}{\mu_1\mu_2}.$$

∎

4. GLOBAL STABILITY

Local asymptotic stability of the equilibrium points has been established in Wikan and Eide [18]. This subsection deals with (i) the global asymptotic stability of $E_1(0,0)$ in both cases of interest and ii) the global asymptotic stability of $E_2(\bar{x}, \bar{y})$ of the system (1.2) with $h(y) = 1/(1+\beta_1 y)$. We do not yet have a global asymptotic stability result of the positive equilibrium in the case when h is exponential.

4.1. Global Stability of the Zero Equilibrium.

The object of study in this subsection is the zero equilibrium of system (1.2). We begin with some notations and a proposition that will be useful in our discussion. The following notations are used throughout the paper:

$$I_x = \liminf_{n\to\infty} x_n \quad\text{and}\quad S_x = \limsup_{n\to\infty} x_n,$$

and

$$I_y = \liminf_{n\to\infty} y_n \quad\text{and}\quad S_y = \limsup_{n\to\infty} y_n,$$

The next proposition, whose proof utilizes the monotonicity of the map related to system (4.11), is instrumental in proving our global results (same type of inequalities connecting limit inferior and superior have been used in Awerbuch et al. [1]).

Proposition 4.1. *Consider the rational system* (4.11). *The following inequalities hold:*

$$\mu_1 S_x \leq \frac{F S_y}{1+\beta_1 S_y} \tag{4.1}$$

and

$$\mu_2 S_y \leq P S_x. \tag{4.2}$$

Combining (4.1) *and* (4.2) *we have*

$$\mu_2 S_y \leq \frac{P F S_y}{\mu_1(1+\beta_1 S_y)}. \tag{4.3}$$

In addition:

$$\mu_1 I_x \geq \frac{F I_y}{(1+\beta_1 I_y)} \tag{4.4}$$

$$\mu_2 I_y \geq P I_x. \tag{4.5}$$

The following lemma will be useful in the sequel.

Lemma 4.2. *Let* $-1 < 1-A < 1$ *and suppose that* $(z_n)_{n\geq 0}$ *is a solution of the second order difference equation*

$$z_{n+1} - A z_n - (1-A) z_{n-1} = 0, \qquad n = 0, 1, 2\ldots \tag{4.6}$$

Then

$$\lim_{n\to\infty} z_n = \frac{(1-A)z_{-1}+z_0}{2-A}$$

Proof. The general solution of equation (4.6) is given by $z_n = c_1 + c_2(A-1)^n$. But $-1 < 1-A < 1$, yields $\lim\limits_{n\to\infty}(A-1)^n = 0$, forcing $\lim\limits_{n\to\infty} z_n = c_1$. Using the initial conditions, c_1 can be found by solving the system of equations $z_0 = c_1 + c_2$ and $z_-1 = c_1 + c_2(A-1)^{-1}$ which gives $c_1 = \dfrac{(1-A)z_{-1}+z_0}{2-A}$ (note that $2-A>0$). The conclusion follows. ∎

The next theorem presents the global asymptotic stability of the extinction equilibrium $E_1(0,0)$ of system (1.2) with h rational and exponential:

Theorem 4.3. *Assume* $R_0 \leq 1$. *Then* $E_1(0,0)$ *of system* (1.2) *is globally asymptotically stable.*

Proof. We distinguish two cases.

Case 1: $R_0 < 1$. Let $(x_n, y_n)_{n\geq 0}$ be an arbitrary solution of system (1.2). It suffices to show that $(x_n, y_n)_{n\geq 0}$ converges to zero. For the sake of contradiction assume $S_y > 0$. It follows from $h(y_n) < 1$ and the first equation that $x_{n+1} \leq F y_n + (1-\mu_1)x_n$ for all $n = 0, 1, \ldots$ By the monotonicity of the map:

$$\mu_1 S_x \leq F S_y \tag{4.7}$$

Also, from the second equation in the system we obtain:

$$\mu_2 S_y \leq P S_x \tag{4.8}$$

Combining (4.7) and (4.8) yields the following inequality:

$$\frac{\mu_1\mu_2 S_y}{P} \leq F S_y \tag{4.9}$$

Since $S_y > 0$, this gives $\mu_1\mu_2 \leq PF$ (which is a contradiction). Thus $S_y = 0$, which triggers $I_y = 0$, $S_x = 0$ and $I_x = 0$ and the conclusion follows.

Case 2: $R_0 = 1$. It suffices to show that $(0, 0)$ is a global attractor. The proof uses the same techniques as in (Awerbuch et al. [2], pp. 472) and we show it for convenience of the reader. The system (1.2) can be changed into the following scalar equation

$$y_{n+1} = (1-\mu_2)y_n + PFh(y_{n-1})y_{n-1} + (1-\mu_2)y_n - (1-\mu_1)(1-\mu_2)y_{n-1}$$

By grouping:

$$y_{n+1} = (2-\mu_1-\mu_2)y_n + [PFh(y_{n-1}) - (1-\mu_1)(1-\mu_2)]y_{n-1} \tag{4.10}$$

Since $h(y_{n-1}) < 1$ and $PF = \mu_1\mu_2$, the following inequalities hold:

$$\begin{aligned} y_{n+1} &= (2-\mu_1-\mu_2)y_n + [PFh(y_{n-1}) - (1-\mu_1)(1-\mu_2)]y_{n-1} \\ &\le (2-\mu_1-\mu_2)y_n + [\mu_1\mu_2 - (1-\mu_1)(1-\mu_2)]y_{n-1} \\ &= (2-\mu_1-\mu_2)y_n + (\mu_1+\mu_2-1)y_{n-1} \end{aligned}$$

Rewriting, one gets:

$$y_{n+1} \le [1-(2-\mu_1-\mu_2)]y_{n-1} + (2-\mu_1-\mu_2)y_n = (1-A)y_{n-1} + Ay_n$$

where $A = 2-\mu_1-\mu_2$. Note that $-1 < 1-A < 1$. For an arbitrary non-negative integer $k \in \{0, 1, \ldots\}$, consider the second order linear difference equation

$$z_{k,n+1} = (1-A)z_{k,n-1} + Az_{k,n}, \qquad n = k, k+1\ldots$$

with initial conditions

$$z_{k,k-1} = y_{k-1} \quad \text{and} \quad z_{k,k} = y_k.$$

By applying Lemma (4.2), it follows that:

$$\lim_{n\to\infty} z_{k,n} = \frac{(1-A)z_{k,k-1} + z_{k,k}}{2-A}$$

Since $y_n \le z_{k,n}$ for all $n \ge k-1$, we have

$$\limsup_{n\to\infty} y_n \le \frac{(1-A)y_{k-1} + y_k}{2-A}$$

For the sake of contradiction suppose that $I_y = \liminf_{n\to\infty} y_n$ and $S_y = \limsup_{n\to\infty} y_n$ are not equal to each other, so $I_y < S_y$. Next we apply Theorem (7.5) (see Appendix), which guarantees that there exists a full limiting sequence $(L_n)_{n=-\infty}^{\infty}$ of $(y_n)_{n\ge0}$ and a subsequence $(y_{k_i})_{i=0}^{\infty}$ of $(y_n)_{n\ge0}$ such that

$$L_0 = I_y \qquad \text{and} \lim_{i\to\infty} y_{k_i-j} = L_{-j} \qquad \text{for} \qquad j = 0, 1.$$

Thus:

$$S_y = \limsup_{n\to\infty} y_n \le \frac{(1-A)L_{-1} + L_0}{2-A} < \frac{(1-A)S_y + S_y}{2-A} = S_y$$

which is a contradiction. Therefore $I_y = S_y$ and since $E_1(0, 0)$ is the only equilibrium in this parameter region, the conclusion follows. ∎

4.2. **Global Stability of the Positive Equilibrium.** In this section, we address the global asymptotic stability behavior of the positive equilibrium. Consider $h(y) = 1/(1+\beta_1 y)$. Then equations in (1.2) read:

$$\begin{cases} x_{n+1} = \dfrac{F}{1+\beta_1 y_n} y_n + (1-\mu_1)x_n \\ \\ y_{n+1} = Px_n + (1-\mu_2)y_n \end{cases} \qquad n = 0, 1, \ldots, \tag{4.11}$$

We begin with the following remark which plays a central role in the proof of the global stability theorem.

Remark 4.1. When $R_0 > 1$, the zero equilibrium becomes unstable and the positive equilibrium appears. We argue that when $R_0 > 1$, both $\liminf_{n\to\infty} x_n$ and $\liminf_{n\to\infty} y_n$ are positive. We can then use the information to conclude that nonnegative solutions of system (4.11) will not approach the zero equilibrium in this region. We make use of a theorem in Kon [13] (see Theorem (7.3) of the Appendix). It is easy to verify that the system is dissipative and forward invariant on the non-negative cone $\mathbb{R}^2_+$. Because $A_{\mathbf{0}} = \mathbf{J}_{(0,0)}$ (see Appendix for its form) is nonnegative and the matrix $(I_2 + A_{\mathbf{0}})^2$ has all entries positive, it follows from Theorem (7.1) that $A_{\mathbf{0}}$ is irreducible. The matrix $A_{\mathbf{0}}$ is nonnegative and irreducible, and therefore by applying the Perron-Frobenius Theorem (see for example Cushing [4]) we have that $A_{\mathbf{0}}$ possesses a positive eigenvalue with magnitude greater than or equal to all other existing eigenvalues. Its eigenvalues are the roots of

$$P(\lambda) = \lambda^2 - [2-\mu_1-\mu_2]\lambda - [PF - (1-\mu_1)(1-\mu_2)]$$

Notice that $\lim_{\lambda\to\infty} P(\lambda) = \infty$, and thus $P(1) < 0$ yields a root greater than 1. But $P(1) = \mu_1\mu_2 - PF$, which is negative when $\mu_1\mu_2 < PF$ or $R_0 > 1$. Thus system (4.11) is p-permanent, and according to the definition (see Appendix), there exists positive constants $\delta > 0$ and $D > 0$ such that $\delta \le \liminf_{n\to\infty}(x_n + y_n) \le \limsup_{n\to\infty}(x_n + y_n) \le D$. Implicitly, we can say that solutions do not tend to the origin under the given restriction $R_0 > 1$. Also, $0 < \delta \le \limsup_{n\to\infty}(x_n + y_n) \le \limsup_{n\to\infty} x_n + \limsup_{n\to\infty} y_n$. Moreover, all the hypotheses in Theorem (7.4) are satisfied, and therefore system (4.11) is c-permanent, meaning that $I_x = \liminf_{n\to\infty} x_n > 0$ and $I_y = \liminf_{n\to\infty} y_n > 0$

Theorem 4.4. *Assume* $R_0 > 1$. *Then the positive solutions* $\{(x_n, y_n)\}_{n\ge 0}$ *of rational system* (4.11) *converge to* $E_2(\bar{x}, \bar{y})$. *Moreover, the positive equilibrium* $(\bar{x}, \bar{y})$ *of rational system* (4.11) *is globally asymptotically stable.*

Proof. Local stability follows from Wikan and Eide ([18], pp.1701). Let $(x_n, y_n)_{n\ge 0}$ be an arbitrary positive solution of system (4.11).To complete the proof, it suffices to show that $(x_n, y_n)_{n\ge 0}$ is a global attractor. Inequalities (4.1) and (4.2) give

$$S_x \le \frac{FS_y}{\mu_1(1+\beta_1 S_y)} \tag{4.12}$$

$$S_y \le \frac{PS_x}{\mu_2} \tag{4.13}$$

Combining (4.12) and (4.13) one has $S_y \leq \dfrac{PFS_y}{\mu_1\mu_2(1+\beta_1 S_y)}$. According to the discussion in the remark, we have that $I_y > 0$. Obviously, $0 < S_y$. Dividing the above inequality by S_y we obtain

$$S_y \leq \frac{1}{\beta_1}\left(\frac{PF}{\mu_1\mu_2} - 1\right) \tag{4.14}$$

Inequality (4.3) gives $I_x \geq \dfrac{FI_y}{\mu_1(1+\beta_1 I_y)}$ which in combination with (4.4) yields

$$\mu_2 I_y \geq PI_x \geq \frac{PFI_y}{\mu_1(1+\beta_1 I_y)}$$

and since I_y is positive we obtain:

$$I_y \geq \frac{1}{\beta_1}\left(\frac{PF}{\mu_1\mu_2} - 1\right) \tag{4.15}$$

From (4.14) and (4.15) we conclude $S_y \leq I_y$ and we are done. We can say that $S_y = I_y = \dfrac{1}{\beta_1}(\dfrac{PF}{\mu_1\mu_2} - 1) = \bar{y}$. On the other hand, $I_x \geq \dfrac{F\bar{y}}{\mu_1(1+\beta_1\bar{y})}$ and $S_x \leq \dfrac{F\bar{y}}{\mu_1(1+\beta_1\bar{y})}$. It follows that $I_x = S_x = \dfrac{F\bar{y}}{\mu_1(1+\beta_1\bar{y})} = \dfrac{\mu_2}{P}\dfrac{1}{\beta_1}(\dfrac{PF}{\mu_1\mu_2} - 1) = \bar{x}$. ∎

Regarding the global asymptotic stability of the exponential system, the following behavior is worth mentioning. When $R_0 > 1$, the zero equilibrium becomes unstable and the positive equilibrium appears. The positive equilibrium is locally asymptotically stable in a subregion of $R_0 > 1$, more specifically when $\mu_1\mu_2 < PF < \mu_1\mu_2 e^{(\mu_1+\mu_2)/\mu_1\mu_2}$ (Wikan and Eide [18]). We conjecture that if $\mu_1\mu_2 < PF < \mu_1\mu_2 e^{(\mu_1+\mu_2)/\mu_1\mu_2}$, the positive equilibrium $E_2(\bar{x}, \bar{y})$ of the exponential model is in fact globally asymptotically stable.

5. STOCHASTIC MODEL

Wikan and Eide [18] attempt to account for the cod stock dynamics through a deterministic model of cod recruitment and cannibalism, which are factors that directly impact cod biomass. They further suggest that attempting to incorporate other influential factors such as those associated with the environment, ecosystem and fishing patterns would make the model too complicated and complex.

An alternative approach to directly incorporating the impact of environmental and other influential factors is to introduce random changes into the existing parameters of the cod stock dynamics model. We note that a significant consequence of the impact of the 'missing' factors associated with environment, ecosystem and fishing patterns on cod biomass is the non-deterministic variations in cod biomass noted by Wikan and Eide. Modeling system parameters as stochastic does not directly identify the mechanisms by which the missing factors influence cod biomass. Obtaining that insight would require the incorporation of factors that Wikan and Eide point out would make the model too complicated and complex. However, introducing stochastic model parameters will provide the opportunity of gaining insight into the consequences on cod biomass of the missing factors to the extent that they influence the model parameter values.

For example, we will incorporate randomness in the fecundity parameter F. Our simulations will exhibit the behavior of cod biomass under the combined influence of the fixed parameter values associated with cod recruitment and cannibalism, as well as the impact of those missing factors that influence the fecundity parameter F. We will present simulation results that document dynamic behaviors under the random fecundity parameter F that are not present in the deterministic model.

A major objective of this simulation study is to determine if the resulting model can better demonstrate the diversity of observed variation in cod biomass while not adding appreciably to the complexity of the model in terms of additional terms and parameters. We believe that the trade-off between model complexity and model interpretability is best served by the introduction of uncertainty in one of the major parameters of the cod stock dynamic model. If we let all the parameters be random, then each sample value of each parameter results in a value of R_0 that is either greater, equal or less than 1 (or greater or less than K). Hence the results will be dictated by R_0 not by which parameters are random. Hence choosing an alternative parameter to randomize would produce analogous observed behavior.

The results presented in the next two sections fall into two distinct categories. The introduction of randomness in the fecundity parameter F introduces a random fluctuation in the location of the non-zero equilibrium point of the immature and mature cod populations. The statistical properties of this non-zero equilibrium point, parameterized by the net reproductive number R_0, are presented in section 5.1.

The statistical properties of the non-zero equilibrium presented in section 5.1 are independent of the dynamics of the cod populations occurring around the equilibrium. Those dynamics are determined by the chosen model parameters. Our interest in simulating the cod population dynamics under a random fecundity parameter is to explore dynamic behavior created as a consequence of the random fecundity parameter fluctuation. Our simulation results are presented in section 5.2

5.1. **Equilibrium Points.**

Consider F to be random with distribution function $G(.)$, where the probability $\Pr(F \leq x) = G(x)$. The equilibrium solution is given by the random point $(\bar{x}, \bar{y})$, where

$$\bar{x} = \frac{\mu_2}{P} h^{-1}\left(\frac{\mu_1\mu_2}{FP}\right), \; \bar{y} = h^{-1}\left(\frac{\mu_1\mu_2}{FP}\right) \tag{5.1}$$

This leads to the following theorem, which characterizes the cumulative distribution function of the net reproductive number R_0 and the joint distribution function of the non-zero equilibrium.

Theorem 5.1. *Let F be a strictly positive random variable taking values in a compact interval $[F_-, F_+]$.*

Let G be an arbitrary cumulative distribution function with compact support $[F_-, F_+]$.

Let h be a positive strictly monotone decreasing function on $\mathbb{R}_+$.

Let $R_- = \frac{PF_-}{\mu_1\mu_2}$ and $R_+ = \frac{PF_+}{\mu_1\mu_2}$.

Recall that

$$R_0 = \frac{P}{\mu_1\mu_2}F, \quad \bar{y} = h^{-1}\left(\frac{1}{R_0}\right), \quad \bar{x} = \frac{\mu_2}{P}\bar{y}$$

where $P > 0$, $0 < \mu_1 < 1$ and $0 < \mu_2 < 1$.

Then

(1) *R_0 is a strictly positive random variable with compact support $[R_-, R_+]$ and cumulative distribution function*

$$\Pr(R_0 \leq r) = G\left(\frac{\mu_1\mu_2}{P}r\right).$$

(2) *If* $R_0 > 1$*, then* $(\bar{x}, \bar{y})$ *is a strictly positive bivariate random variable with compact support* $\left[\frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_-}\right), \frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_+}\right)\right]$ *and joint cumulative distribution function*

$$\Pr\left(\bar{x} \le x, \bar{y} \le y\right) = \begin{cases} 0 & \textit{if } (x,y) \textit{ in region A} \\ G\left(\frac{\mu_1\mu_2}{P} \frac{1}{h\left(\frac{Px}{\mu_2}\right)}\right) & \textit{if } (x,y) \textit{ in region B or D} \\ G\left(\frac{\mu_1\mu_2}{P} \frac{1}{h(y)}\right) & \textit{if } (x,y) \textit{ in region C} \\ 1 & \textit{if } (x,y) \textit{ in region E} \end{cases}$$

where the regions are defined by

region A: $y < h^{-1}\left(\frac{1}{R_-}\right)$ *or* $x < \frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_-}\right)$

region B: $h^{-1}\left(\frac{1}{R_-}\right) < y < h^{-1}\left(\frac{1}{R_+}\right)$ *and* $\frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_-}\right) < x < \left(\frac{\mu_2}{P}\right) y$

region C: $h^{-1}\left(\frac{1}{R_-}\right) < y < h^{-1}\left(\frac{1}{R_+}\right)$ *and* $x \ge \frac{\mu_2}{P} y$

region D: $h^{-1}\left(\frac{1}{R_+}\right) < y$ *and* $x < \frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_+}\right)$

region E: $h^{-1}\left(\frac{1}{R_+}\right) < y$ *and* $x \ge \frac{\mu_2}{P} h^{-1}\left(\frac{1}{R_+}\right)$

Proof. For R_0,

$$\begin{aligned} \Pr\left(R_0 \le r\right) &= \Pr\left(\frac{P}{\mu_1\mu_2} F \le r\right) \\ &= \Pr\left(F \le \left(\frac{\mu_1\mu_2}{P}\right) r\right) \\ &= G\left(\frac{\mu_1\mu_2}{P} r\right) \end{aligned}$$

For the joint distribution of $(\bar{x}, \bar{y})$,

$$\Pr\left(\bar{x} \le x, \bar{y} \le y\right) = \Pr\left(\bar{y} \le \min\left(y, \frac{P}{\mu_2} x\right)\right)$$

and the result follows from

$$\begin{aligned} \Pr\left(\bar{y} \le y\right) &= \Pr\left(h^{-1}\left(\frac{1}{R_0}\right) \le y\right) \\ &= \Pr\left(\frac{1}{R_0} \ge h(y)\right) \quad \text{by monotonicity of } h \\ &= \Pr\left(R_0 \le \frac{1}{h(y)}\right) \\ &= G\left(\frac{\mu_1\mu_2}{P} \frac{1}{h(y)}\right) \end{aligned}$$

The compact support of $(\bar{x}, \bar{y})$ follows from R_0, $\bar{x}$ and $\bar{y}$ all being strictly increasing functions of F. ∎

The following corollary characterizes the marginal distribution function of the immature, mature and total cod populations.

Corollary 5.2. *Under the conditions of theorem 5.1,*

(1) $\bar{x}$ *is a strictly positive random variable with compact support*

$$\left[\frac{\mu_2}{P}h^{-1}\left(\frac{1}{R_-}\right), \frac{\mu_2}{P}h^{-1}\left(\frac{1}{R_+}\right)\right]$$

and cumulative distribution function

$$\Pr\left(\bar{x} \le x\right) = G\left(\frac{\mu_1\mu_2}{P}\frac{1}{h\left(\frac{Px}{\mu_2}\right)}\right).$$

(2) $\bar{y}$ *is a strictly positive random variable with compact support*

$$\left[h^{-1}\left(\frac{1}{R_-}\right), h^{-1}\left(\frac{1}{R_+}\right)\right]$$

and cumulative distribution function

$$\Pr\left(\bar{y} \le y\right) = G\left(\frac{\mu_1\mu_2}{P}\frac{1}{h(y)}\right).$$

(3) $\bar{x} + \bar{y}$ *is a strictly positive random variable with compact support*

$$\left[\left(1 + \frac{\mu_2}{P}\right)h^{-1}\left(\frac{1}{R_-}\right), \left(1 + \frac{\mu_2}{P}\right)h^{-1}\left(\frac{1}{R_+}\right)\right]$$

and cumulative distribution function

$$\Pr\left(\bar{x} + \bar{y} \le s\right) = G\left(\frac{\mu_1\mu_2}{P}\frac{1}{h(\hat{s})}\right), \ \hat{s} = \frac{s}{1 + \frac{\mu_2}{P}}$$

(4) *The first two moments of* $\bar{x} + \bar{y}$ *are*

$$E(\bar{x} + \bar{y}) = \left(1 + \frac{\mu_2}{P}\right) * E\left(h^{-1}\left(\frac{1}{R_0}\right)\right)$$

$$\mathit{Var}(\bar{x} + \bar{y}) = \left(1 + \frac{\mu_2}{P}\right)^2 * \mathit{Var}\left(h^{-1}\left(\frac{1}{R_0}\right)\right)$$

Proof. The first two results follow by taking limits as x (respectively y) approaches infinity in the joint distribution of $(\bar{x}, \bar{y})$. The last two results follow from the fact that $\bar{x} = \frac{\mu_2}{P}\bar{y}$ ∎

It is worth noting in the above results that the support regions for the various distributions depending only on the parameters P, F, μ_1 and μ_2 of the dynamic system (1.2). The randomness in the equilibrium point and its statistical properties are due exclusively to the randomness in F.

Remark 5.1. The Deriso-Schnute general recruitment function (from which the Ricker and Beverton-Holt functions are special cases) is of the form

$$h(y) = F(1 - \gamma\beta y)^{\frac{1}{\gamma}}$$

It is a simple exercise to show that h is a strictly monotonic decreasing function for all $\gamma \le 0$. Thus our results in Theorem 5.1 and Corollary 5.2 hold for any Deriso-Schnute recruitment function with $\gamma \le 0$.

Example 5.3. Consider the following example, which is the basis for one of our simulations. Let the fecundity parameter F have a uniform distribution on the interval $[a, b]$ where the interval

$[a, b]$ is chosen such that $\mu_1\mu_2 \leq Pa$ (an example of this is given in section 5.3). Assume $h(y)$ is the Ricker recruitment function. Then the uniform distribution for F is

$$G(s) = \frac{s-a}{b-a} \quad for \quad s \in [a, b]. \tag{5.2}$$

For (x, y) in the compact region

$$\frac{\mu_2}{\beta_1 P} \ln\left(\frac{aP}{\mu_1\mu_2}\right) \leq x \leq \frac{\mu_2}{\beta_1 P} \ln\left(\frac{bP}{\mu_1\mu_2}\right)$$
$$\frac{1}{\beta_1} \ln\left(\frac{aP}{\mu_1\mu_2}\right) \leq y \leq \frac{1}{\beta_1} \ln\left(\frac{bP}{\mu_1\mu_2}\right)$$

the joint distribution of $(\bar{x}, \bar{y})$ is given by the piecewise defined function

$$\Pr(\bar{x} \leq x, \bar{y} \leq y) = \begin{cases} \left(\frac{1}{b-a}\right)\left(\frac{\mu_1\mu_2}{P} e^{\left(\frac{x\beta_1 P}{\mu_2}\right)} - a\right) & \text{if } x \leq \frac{\mu_2 y}{P} \\ \left(\frac{1}{b-a}\right)\left(\frac{\mu_1\mu_2}{P} e^{y\beta_1} - a\right) & \text{if } x > \frac{\mu_2 y}{P} \end{cases}$$

One of the parameter sets we use in our simulations entails setting $[a, b] = [10, 12]$, $\mu_1 = \mu_2 = 0.2$, $P = 0.8$ and $\beta_1 = 2.2951$. The corresponding joint distribution for the equilibrium $(\bar{x}, \bar{y})$ is

$$\Pr(\bar{x} \leq x, \bar{y} \leq y) = \begin{cases} 0.025e^{(9.18x)} - 5 & \text{if } x \leq 0.25y \\ 0.025e^{(2.295y)} - 5 & \text{if } x > 0.25y \end{cases}$$

for $0.577 \leq x \leq 0.597$ and $2.309 \leq y \leq 2.388$. It is easy to show that in this case the expected value of the equilibrium point is $E(\bar{x}) = 0.5874$ and $E(\bar{y}) = 2.3495$.

5.2. **Stability.**

We have presented in section 5.1 a probabilistic description of the impact of the uncertainty in the fecundity parameter F on the non-zero equilibrium. We now consider the impact of an uncertain F on system dynamics.

For a fixed, deterministic value of F, the global asymptotic stability of the limiting solution to (1.2) in the case of the Beverton-Holt recruitment function has been established. If we consider the Ricker recruitment function, the local asymptotic stability conditions for the limiting solution of (1.2) reduce to

$$1 < R_0 < K \tag{5.3}$$

(Wikan and Eide [18]), where $R_0 = \dfrac{PF}{\mu_1\mu_2}$ and $K = e^{\left(\frac{1}{\mu_1} + \frac{1}{\mu_2}\right)}$. The system is unstable when $R_0 > K$ and the stability is lost through a Hopf bifurcation (Wikan and Eide [18]). It is of interest to note that for our model assumption that $\beta_2 = \beta_3 = 0$, the stability of the equilibrium solution depends only on the parameters μ_1, μ_2, P and F and that the cannibalism parameter β_1 plays no role.

Condition (5.3) determines the stability property of the solution of the deterministic system (1.2) with a Ricker recruitment function. If we now allow F to be random, with its value at each iteration of the dynamic system being a sample from its assumed probability distribution, then the observed dynamic stability properties will be dictated by the distribution of F and the sample F iterates which satisfy (5.3). This results in local stability behavior that is different than that observed in the deterministic case.

We consider three scenarios for the values of a random fecundity parameter F.

If F satisfies condition (5.3) for all values of F in its compact range (i.e. $1 < R_0 < K$), then the system exhibits perturbations on dynamic stability that mirror the stability of the deterministic system modulo the fact that the equilibrium point is now random.

If F violates the right hand side in (5.3) for all values of F in its compact range (i.e. $R_0 > K$)), then the system exhibits perturbations on dynamic instability that mirror the instability of the deterministic case modulo the fact that the equilibrium point is random.

The interesting new behavior which can arise from the stochastic model occurs when the left hand inequality in (5.3) holds for all F in its compact range (i.e. $R_0 > 1$), but the distribution of F is such that there is a positive probability of F satisfying the right hand inequality in (5.3) and a positive probability of violating the right hand inequality in (5.3) (i.e. both $R_0 < K$ and $R_0 > K$ can occur). In this case we have a system that demonstrates stable behavior some of the time and unstable behavior some of the time.

5.3. **Simulations.** We use simulations to demonstrate the nature of the system dynamics in each of our three scenarios. We assume that F has a uniform distribution on the interval $[10, 12]$. Choice of a uniform distribution suggests no a-priori knowledge of the value of F other than it is reasonable to expect it to be within a finite interval. The results obtained in this case are not specific to the choice of a uniform distribution for F. If the assumed distribution of F is to be changed to a non-uniform distribution with compact support, the probabilities of being on one side or the other of the stability boundary might change, but the actual dynamic behavior is preserved as with a uniform distribution. Thus, other distributions for F that satisfy the restriction that $F > 0$ almost everywhere are plausible to yield similar results if their region of positive support has the same relationship with the condition (5.3) as indicated in the examples below.

The cannibalism parameter β_1 will be fixed at 2.2951 for each scenario. The remaining parameters (μ_1, μ_2 and P) will be chosen to meet the requirements of each scenario.

Each simulation consists of 10,000 iterations of the discrete dynamic system. Both our phase plots and our time series plots display the last 200 iterates. The phase plot relates the immature population to the mature population, while the time series plots display the total population as it evolves over time.

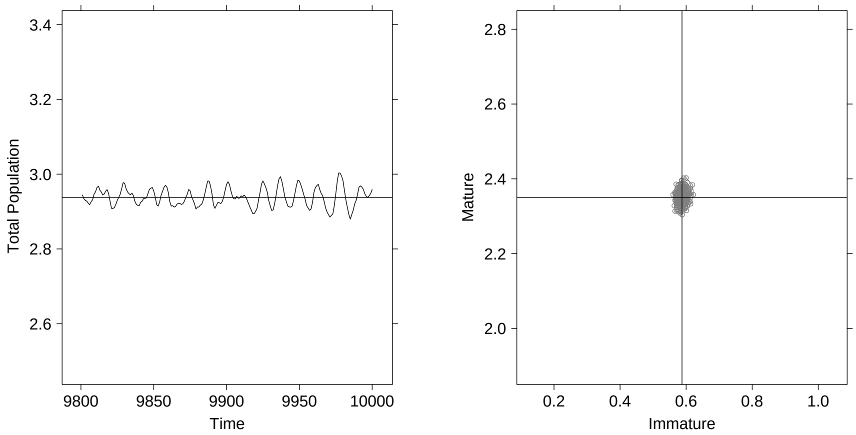
5.3.1. *Stability.* Consider the case when $\beta_1 = 2.2951$, $\mu_1 = \mu_2 = 0.20$, and $P = 0.80$. Then (5.3) is satisfied for all values of F in the interval $[10, 12]$ (i.e. $1 < R_0 < K$). The equilibrium solution is given in Example 5.3.

Here it is easy to see the effect of the random nature of F both in the phase plot and in the time series plot of the total population. Note that the behavior of the stochastic model mirrors the behavior of the deterministic system but does not converge to the equilibrium point. Rather, the convergence is to the support of the equilibrium point. Clearly there is variation in the total biomass that is not evidenced in the deterministic system.

5.3.2. *Instability.* In order to simulate an unstable system, we set the model parameters for β_1, P and F as above, but let $\mu_1 = \mu_2 = 0.99$. The right hand inequality in (5.3) is then violated for all values of F in the compact range $[10, 12]$ (i.e. $R_0 > K$). This creates an unstable system. For this set of parameters, the equilibrium has compact support $[1.13, 1.23]$ for $\bar{x}$ and $[0.915, 0.994]$ for $\bar{y}$ and expected values $E(\bar{x}) = 1.1827$ and $E(\bar{y}) = 0.956$. The positive equilibrium is a repelling equilibrium point and the system dynamics result in quasi-periodic loops around the equilibrium point. The time series plot and phase plot for these simulations are shown in Figure 2b and 2c respectively.

5.3.3. *Mixed.* We now consider the case where the probability distribution of the fecundity parameter F is such that there is a positive probability that $R_0 < K$ and a positive probability that $R_0 > K$.

To simulate this case, we set the model parameters P and β_1 as before and set $\mu_1 = 0.6$ and $\mu_2 = 0.8$. Clearly the left side of (5.3) is satisfied for all F in the compact interval $[10, 12]$.



(A) Time Series (B) Phase Plot

FIGURE 1. The phase plot in Figure 1 indicates the limiting behavior of the solution to (1.2) when F is random (the elliptic-shaped values) and compares that with the limiting behavior when F is fixed at 11 (marked as the intersection of the cross-hairs). The horizontal line in the time series plot indicates the deterministic system total population value during the last 200 iterations out of 10,000 iterations, and the sinusoidal-like curve is the total population fluctuations due to the randomness in F.

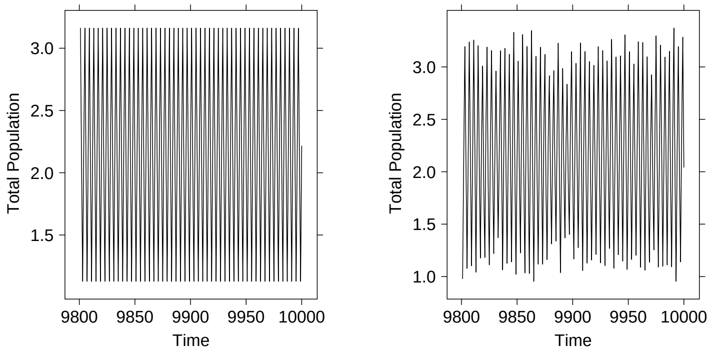
The right side of (5.3) is $K = 18.4796$. Sample values of $F < 11.09$ induce stable behavior ($R_0 < K$) while sample values of $F > 11.09$ induce unstable behavior ($R_0 > K$). For this set of parameters, the support for the equilibrium is $1.23 \leq \bar{x} \leq 1.31$ and $1.23 \leq \bar{y} \leq 1.31$ and the expected value of the equilibrium point is $E(\bar{x}) = E(\bar{y}) = 1.267$.

This results in a system dynamic that experiences both stable and unstable behavior: the system can go through periods where it is trying to converge (noisily) to a random equilibrium point (when $R_0 < K$) and then experience periods where it is trying to converge (noisily) to a random limit cycle around the equilibrium point (when $R_0 > K$). This is a dynamic behavior that is not manifest in any deterministic model with a fixed F chosen from the interval $[10, 12]$. The phase plot and time series plot for these simulations are shown in Figure 3.

6. CONCLUSIONS

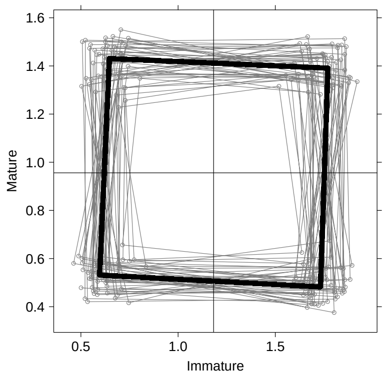
The discrete time model discussed in the current paper was proposed by Wikan and Eide [18]. The nonlinearities in the model are of rational and exponential type, thus creating a rational and respectively exponential system of difference equations. While the local asymptotic stability has been addressed by the aforementioned authors, the global asymptotic stability needed investigation. In this paper we proved (i) global asymptotic stability of the extinction equilibrium of both rational and exponential systems and (ii) global asymptotic stability of the positive equilibrium of the rational system.

The nature of the physical system being modeled suggests that a deterministic model is limited in its ability to reproduce the type of variations in cod biomass that are observed in historical data. And yet there is a value in being able to utilize as simple a model as possible to allow for understanding the system behavior. This model attempts to satisfy these needs. To gain insight into the potential impact of uncertainty on the behavior of the cod biomass, we suggested a stochastic model. While there are many ways in which stochasticity enters the system (Dennis



(A) Deterministic Time Series

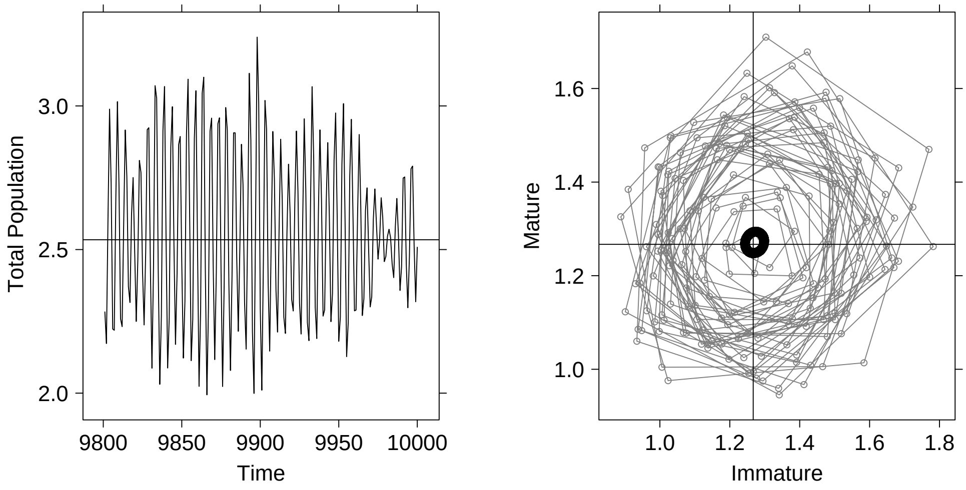
(B) Random Time Series



(C) Phase Plot

FIGURE 2. This graph compares the simulated system phase plot and time series to that of an equivalent unstable deterministic system with fecundity parameter F fixed at 11. Figure 2c displays the deterministic system asymptotic phase plot behavior as the solid black square, surrounded by the random system gray cycles. The behavior of the stochastic system demonstrates the same quasi-periodic behavior around the equilibrium point as the deterministic system. Figure 2a is the time series of total population, which displays a uniformity that becomes more variable in the dynamics shown in Figure 2b of the random system.

et al. [7], Henson et al. [9], Kesinger and Allen [12]), our approach is to make the fecundity parameter random. This approach is mostly based on the fact that environmental conditions and other influential factors such as ecosystem and finishing patterns can affect the immature and mature cod population. Allowing parameters to be random can provide variation to the equilibrium solution. In addition, it can add an element of random variation to the system behavior that may account for some of the empirically observed biomass fluctuation. Of particular interest in the random parameter model is the possibility of system behavior that mixes the stable and unstable behaviors that exist in the deterministic domain. Numerical simulations in Section 5 suggest that the dynamics of the stochastic model exhibit a mixture of the dynamics observed in the deterministic model. In a sense, this makes the system proposed by Wikan and Eide "*amenable to the tools of discrete dynamical systems and statistical techniques*" (S. M. Henson



(A) Time Series (B) Phase Plot

FIGURE 3. Mixed System: This graph illustrates the random system behavior in the mixed scenario. The phase plot Figure 3b superimposes the fixed parameter system behavior when $F = 11.09$, which is the solid black inner circles, against the random parameter system gray cycles. The time series plot Figure 3a for the random system demonstrates a pulsing behavior reflective of 'flipping' between the stable and unstable behaviors which is not evident in the unstable deterministic system dynamic. The phase plot for the random system also shows how this alternating behavior differs from that of the unstable deterministic system. This behavior of the random system suggests an additional dynamic behavior that is absent in the deterministic model.

[9]). The results also suggest that this model may in fact be used to represent a broader range of applications.

7. APPENDIX

7.1. **General Framework.** We view system (1.2) in a matrix form:

$$\mathbf{X}_{n+1} = A_{X_n}\mathbf{X}_n \tag{7.1}$$

where $n = 0, 1, 2, \ldots$ and $\mathbf{X}_n = (x_n, y_n)^T$. The entries of matrix A_{X_n} are denoted by a_{ij} and they are continuous functions of x_n, and y_n. The nonlinear matrix structure is

$$A_{\mathbf{X}} = \begin{pmatrix} 1-\mu_1 & Fh(y) \\ P & 1-\mu_2 \end{pmatrix} \quad \text{and} \quad X = \begin{pmatrix} x \\ y \end{pmatrix}$$

The matrix $A_{\mathbf{X}}$ has all entries nonnegative. The function h can be replaced by two forms, $h = 1/(1+\beta_1 y)$ and $h(y) = e^{-\beta_1 y}$. Note that $h(0) = 1$ for both exponential and rational functions. Thus:

$$A_{\mathbf{0}} = \mathbf{J}_{(0,0)} = \begin{pmatrix} 1-\mu_1 & F \\ P & 1-\mu_2 \end{pmatrix}.$$

7.2. **Definitions and Useful Theorems.** In this subsection we list the definitions and the theorems used throughout the paper. The following five definitions, adapted to the two dimensional case, are extracted from Kon ([13], p. 617-620). The nonnegative cone (the set of points in $\mathbb{R}^2$ with $x_n \geq 0, y_n \geq 0$) is denoted by $\mathbb{R}^2_+$.

Definition 7.1. The boundary of the nonnegative cone is denoted by **bd** $\mathbb{R}^2_+ = \{x \in \mathbb{R}^2_+ : x_n y_n = 0\}$

Definition 7.2. System (7.1) is said to be *p-permanent* if there exist positive constants $\delta > 0$ and $D > 0$ such that

$$\delta \leq \liminf_{n\to\infty}(x_n + y_n) \leq \limsup_{n\to\infty}(x_n + y_n) \leq D$$

for all solutions with initial conditions in $\mathbb{R}^2_+ - \{(0,0)\}$

Definition 7.3. System (7.1) is said to be *c-permanent* if there exist positive constants $\delta > 0$ and $D > 0$ such that

$$\delta \leq \liminf_{n\to\infty} x_n \leq \limsup_{n\to\infty} x_n \leq D$$

and

$$\delta \leq \liminf_{n\to\infty} y_n \leq \limsup_{n\to\infty} y_n \leq D$$

for all solutions with initial conditions in $\mathbb{R}^2 - \{(0,0)\}$.

Definition 7.4. System (7.1) is said to be *dissipative* if there exists a positive constant $D > 0$ such that $\limsup_{n\to\infty}(x_n + y_n) \leq D$ for all solutions with initial conditions in $\mathbb{R}^2_+$.

Definition 7.5. Consider two matrices $A = (a_{ij})$ and $B = b_{ij}$. We have that sign(A)=sign(B) if a_{ij} and b_{ij} have the same sign: $-$,0 or $+$.

A very useful test for a matrix to be irreducible is given in Varga [17]:

Theorem 7.1 (Varga [17] (p. 6)). *A is a nonnegative irreducible $n \times n$ matrix if and only if* $(I_n + A)^{n-1} > 0$.

Theorem 7.2 (Kon [13] (p.625) or Theorem 13.8 in Gantmacher [8]). *A nonnegative square matrix A is primitive if and only if there exists an integer $k \geq 1$ such that $A^k > 0$.*

The next two theorems applied to a two dimensional case are extracted from Kon [13]. As a general framework consider the following four hypotheses (H1)-(H4) (see Kon [13] (p.618)).

(H1) each $a_{ij}(\mathbf{X})$ is continous
(H2) $A_{\mathbf{X}}\mathbf{X} \geq 0$ for all $\mathbf{X} \geq 0$
(H3) $A_{\mathbf{X}}\mathbf{X} > 0$ for all $\mathbf{X} > 0$
(H4) System (7.1) is dissipative

Theorem 7.3 (see Theorem 3.2 in Kon [13] (p.620)). *Assume that (H1)-(H4) hold. Suppose that the matrix $A_{\mathbf{0}}$ is irreducible. System* (7.1) *is p-permanent if $A_{\mathbf{0}}$ has an eigenvalue λ with* $|\lambda| > 1$ *(i.e the magnitude of the dominant eigenvalue of $A_{\mathbf{0}}$ is greater than one).*

Theorem 7.4 (see Theorem 4.3 Kon [13] (p.621)). *Assume hypotheses (H1)-(H4) hold: Suppose that $A_{\mathbf{X}}$ is irreducible for all $\mathbf{X} \in \mathbb{R}^2_+$, sign $A_{\mathbf{X}}$=sign $A_{\mathbf{0}}$ holds for all $\mathbf{X} \in bd\mathbb{R}^2_+$ and system* (7.1) *is p-permanent. The system* (7.1) *is c-permanent if and only if $A_{\mathbf{0}}$ is primitive.*

The following result, very useful in addressing the global convergence of solutions, is from Karakostas [11]. We make use of it in Theorem (4.3) (taking $k = 1$).

Theorem 7.5 (Karakostas [11]). *Let* $\{x_n\}_{n=-k}^{\infty}$ *be a solution to the difference equation*

$$x_{n+1} = f(x_n, \ldots, x_{n-k}) \tag{7.2}$$

where $f : J^{k+1} \to J$ *is a continous function and* J *is an interval of real numbers. The initial conditions* $x_{-k}, x_{-k+1}, \ldots, x_0 \in J$. *Set* $I = \liminf_{n\to\infty} x_n$ *and* $S = \limsup_{n\to\infty} x_n$, *and suppose that* $I, S \in J$. *Let* $\mathcal{L}_0$ *be a limit point of the sequence* $\{x_n\}_{n=-k}^{\infty}$. *Then the following statements are true.*

(1) *There exists a solution* $\{L_n\}_{n=-\infty}^{\infty}$ *for the difference equation* (7.2)*, called a full limiting sequence of* $\{x_n\}_{n=-k}^{\infty}$*, such that* $L_0 = \mathcal{L}_0$*, and such that for every* $N \in \{\ldots, -1, 0, 1, \ldots\}$*,* L_N *is a limit point of* $\{x_n\}_{n=-k}^{\infty}$*. In particular,*

$$I \le L_N \le S \quad \text{for all} \quad N \in \{\ldots, -1, 0, 1, \ldots\}.$$

(2) *For every* $i_0 \in \{\ldots, -1, 0, 1, \ldots\}$*, there exists a subsequence* $\{x_{r_i}\}_{i=0}^{\infty}$ *of* $\{x_n\}_{n=-k}^{\infty}$ *such that*

$$L_N = \lim_{i\to\infty} x_{r_i+N} \quad \text{for every} \quad N \ge i_0.$$

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