

Non-linear Population Models with Adult-Based Density-Dependence

Terence R. Blows and Bianca A. Luedeker

*Department of Mathematics and Statistics,
 Box 5717, Northern Arizona University, Flagstaff, AZ 86011
 E-mail: Terence.Blows@nau.edu*

ABSTRACT We consider age-structured population models in which density dependent effects are based on the number of adults and not on total population size. This represents, for example, a population whose size is regulated by a limited number of territories of optimal habitat. We model this in three different ways, obtaining results which vary in the complexity of their dynamics.

KEYWORDS: Population modeling; age-structured models.

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1. INTRODUCTION

It is well known that linear age-structured post-breeding models in which all adults are lumped into a single class have the form (Williamson [1]):

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ \dots \\ N_{k-1}(t+1) \\ N_k(t+1) \\ N_A(t+1) \end{bmatrix} = \begin{bmatrix} 0 & \dots & 0 & 0 & P_k f_{k+1} & sm \\ P_0 & \dots & 0 & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & p_{k-2} & 0 & 0 & 0 \\ 0 & \dots & 0 & p_{k-1} & 0 & 0 \\ 0 & \dots & 0 & 0 & P_k & s \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ \dots \\ N_{k-1}(t) \\ N_k(t) \\ N_A(t) \end{bmatrix} \quad (1)$$

Here N_0 indicates the number of newborns, $N_1 - N_k$ the number in each juvenile (non-breeding) age-class and N_A the number of adults. We refer to individuals in age-class N_k as sub-adults as these will breed in the following time step. In the case where $p_k = s$ and $f_{k+1} = m$, so that sub-adult parameters are the same as for adults, these two classes can be combined into class $N_{\bar{A}}$ simplifying the model to:

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ \dots \\ N_{k-1}(t+1) \\ N_{\bar{A}}(t+1) \end{bmatrix} = \begin{bmatrix} 0 & \dots & 0 & 0 & sm \\ p_0 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & p_{k-2} & 0 & 0 \\ 0 & \dots & 0 & p_{k-1} & s \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ \dots \\ N_{k-1}(t) \\ N_{\bar{A}}(t) \end{bmatrix} \tag{2}$$

Non-linear terms must be added to the model to limit population growth and to introduce *carrying capacity*, but there are amyriad of ways in which this can be done. Firstly, there is a choice in which non-linear function should be used. Here we choose a discrete *logistic non-linearity* (also called *Beverton-Holt*) for the dinsity dependence (e.g., Leslie[2]):

$$\phi(x) = (1 + \beta x)^{-1} \tag{3}$$

The reason for this choice is based solely on a desire for relatively simple dynamics. It is well known that the *Ricker* type choice $\phi(x) = e^{-\alpha x}$ (e.g., Smouse & Weiss [3]) is more likely to lead to *exotic dynamics*. Another option lies in the choice of independent variable for the function ϕ . It is generally accepted that a weighted function of population sizes in the age-classes be used and examples include dependence on the total number of individuals (for example Pykh and Eframova [4] and Ugarcovici and Weiss [5]) and on the number of newborns (DeAngelis, Svoboda, Christensen and Vaughan [6]). Here, we select different choice and use the *number of adults* (N_A in (1) or $N_{\bar{A}}$ in (1.2)).

Motivation for this choice is as follows: Consider a bird species in which a critical regulator of population size in a given habitat patch is the number of optimal breeding sites. This patch will support a number of breeding pairs optimal habitat, but any excess adults will be forced into either settling for a site of poorer quality or moving elsewhere. We model these conditions by applying non-linearity into the relevant part of model (2) or (1):

- **Adult Survivorship:** We assume that fewer adults survive, at least in the area under consideration, due to competition for primary territories. The survivorship probabilities p_k and s are modified by density dependent factors. We assume that the survivorship of newborns and juveniles is unaffected.
- **Breeding Success:** We assume that the average number of successful eggs diminishes with adults forced into territories of poorer quality. The parameter m is modified by a density dependent factor.
- **Newborn Survivorship:** We keep the number of successful eggs as a density independent term, but modify survival of the newborns through the first year of life, p_0 , with a density dependent factor.

In Sections 2-4, we consider these scenarios using the simpler model (2). In Section 5, we apply model (1) to the case of survivorship of both adults and sub-adults. We establish some results, provide numerical evidence for others, but leave many questions unanswered. The intention is to illustrate a diversity of results rather than to carry out a thorough analysis as in, e.g., Pykh and Eframova [4] or Wikan and Mjølhus [7].

2. ADULT SURVIVORSHIP SCENARIO

Consider model (1.2) in which the non-linearity lies in adult survivorship:

$$s = \frac{s'}{1 + \beta N_{\bar{A}}(t)} \tag{4}$$

where β and s' are positive constants with $0 < s' \leq 1$. The following result holds:

Theorem 2.1: Consider (2) in which p_0, p_1, \dots, p_{k-1} and m are constants, $0 < p_i \leq 1$ for $i = 0, 1, \dots, k - 1$, $0 < m$, and s is given by (4) where $0 < s' \leq 1$ and β is a positive constant. Let $c = mp_0 p_1 \dots p_{k-1}$ and $R_0 = \frac{cs'}{1 - s'}$. Then:

1. If $R_0 \leq 1$, then no positive equilibrium exists and the population will become extinct.
2. If $R_0 > 1$, then there is a unique positive equilibrium, and this carrying capacity is stable.

Proof: It is easy to show that in the linear case ($\beta = 0$), the characteristic equation is given by $h(\lambda) = (-1)^{k+1} [1^{k+1} - s' \lambda^k - s' c]$. Since $h(\lambda)$ has a unique non-zero turning point between 0 and 1, Perron-Frobenius theory implies that the stability of the origin is determined by the sign of $h(1)$. It follows that the origin (the *extinction equilibrium*) is stable if and only if $cs' + s' - 1$. This may be written in terms of *net reproductive number* R_0 (see Cushing [8, p. 28]) as $R_0 < 1$. That the origin is *globally asymptotically stable* follows from Theorem 1.2.1 in Cushing [8, p. 18].

To reduce the number of parameters in the non-linear model, we apply the change of variables $N_{\bar{A}} \rightarrow \beta N_{\bar{A}}, N_i \rightarrow \beta p_{k-1} p_{k-2} \dots p_i N_i$ for $i = 0, 1, \dots, k$ to (2). This produces the model:

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ \dots \\ N_{k-1}(t+1) \\ N_{\bar{A}}(t+1) \end{bmatrix} = \begin{bmatrix} 0 & \dots & 0 & 0 & \frac{cs'}{1 + N_{\bar{A}}(t)} \\ 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & 0 & 0 \\ 0 & \dots & 0 & 1 & \frac{s'}{1 + N_{\bar{A}}(t)} \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ \dots \\ N_{k-1}(t) \\ N_{\bar{A}}(t) \end{bmatrix}$$

where $c = \beta p_{k-1} p_{k-2} \dots p_1 p_0$. Solving for non-zero equilibria gives uniquely

$$N_0 = N_1 = \dots = N_{k+1} = \frac{c(cs' + s' - 1)}{c + 1}; N_{\bar{A}} = (cs' + s' - 1)$$

This equilibrium is non-negative providing $cs' + s' - 1$ ($R_0 > 1$) which is precisely when the origin is unstable. (The existence of a positive equilibrium also follows from Theorem 1.2.8 in Cushing [8, p. 30].) The Jacobian matrix evaluated at the non-zero (*carrying capacity*) equilibrium is given by the non-negative matrix:

$$\begin{bmatrix} 0 & \dots & 0 & 0 & \frac{c}{(c+1)^2 s'} \\ 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & 0 & 0 \\ 0 & \dots & 0 & 1 & \frac{1}{(c+1)^2 s'} \end{bmatrix}$$

which has characteristic equation $h(\lambda) = (-1)^{k+1} \left(\lambda^{k+1} - \frac{1}{(c+1)^2 s'} \lambda^k - \frac{c}{(c+1)s'} \right)$. As with the linear model, Perron-Frobenius theory implies that stability is determined by the sign of $h(1) = (-1)^k \left(\frac{cs' + s' - 1}{s'(c+1)} \right)$ and the result follows.

Note that the result in part 2 of the theorem is only local and does not imply the global stability of the carrying capacity equilibrium. However, numerical work seems to indicate that this equilibrium is globally asymptotically stable, i.e. that any solution with non-zero initial conditions will tend to this with time.

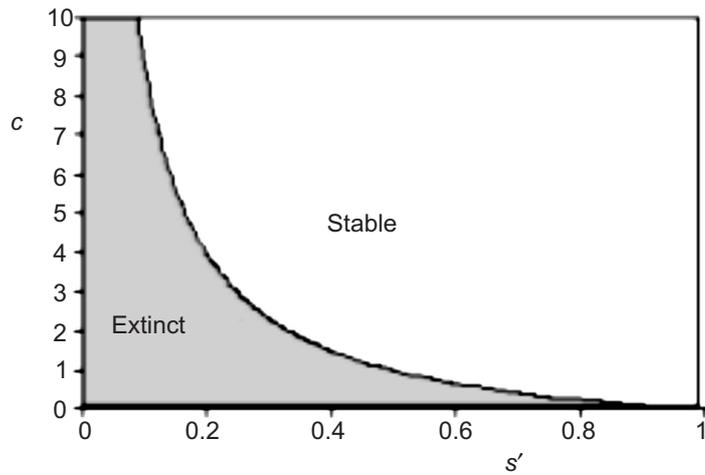


Fig. 1 Regions in the $s' - c$ plane for which solutions go extinct or appear numerically to tend to a stable carrying capacity. The boundary, on which a transcritical

bifurcation occurs, is given by $c = \frac{1 - s'}{s'}$.

3. BREEDING SUCCESS SCENARIO

Consider (2) in which the non-linearity lies in the fecundity m :

$$m = \frac{m'}{1 + \beta N_{\bar{A}}(t)}, \tag{5}$$

(where m and β are positive constants) was previously considered by Fisher and Goh [9]. They show that in this case, a population that does not go extinct tends to a unique stable carrying capacity. We state the result formally below and note that this is stronger than Theorem 2.1 since global asymptotic stability is proved. Fisher and Goh's proof uses a Liapunov function applied to a delay difference equation equivalent to (2).

Theorem 3.1: Consider (2) in which p_0, p_1, \dots, p_{k-1} and s are constants, $0 < p_i \leq 1$ for $i = 0, 1, \dots, k - 1$, $0 < s < 1$ and m is given by (5) where β and m' are positive constants. Let $c = m' p_0 p_1 \dots p_{k-1}$ and $R_0 = \frac{cs}{1 - s}$. Then:

- (1) If $R_0 \leq 1$ no positive equilibrium exists and the population will become extinct.
- (2) If $R_0 > 1$ there is a positive equilibrium, and this carrying capacity is stable. Moreover all solutions tend to this positive carrying capacity in future time.

The bifurcation diagram for this scenario is the same as that given in Fig. 1 except s replaces s' as the variable along the horizontal axis.

4. NEWBORN SURVIVORSHIP SCENARIO

This scenario is the most complex for a model of type (1.2); the reason being that the $N_{\bar{A}}$ (adult) density-dependent term multiplies an N_0 term and not an $N_{\bar{A}}$ term in the matrix equation. In fact the dynamics is quite complex even when $k = 2$.

Theorem 4.1: Consider

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & ms \\ p_0 & 0 & 0 \\ 1 + \beta N_2(t) & p_1 & s \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \end{bmatrix} \tag{6}$$

where p_0, p_1, s and m are constants, $0 < p_0, p_1 \leq 1$, $0 < s < 1$ and m and β are positive constants. Let $c = mp_0 p_1 s$ and $R_0 = \frac{c}{1 - s}$. Then:

- (1) If $R_0 \leq 1$, then no positive equilibrium exists and the population will become extinct.
- (2) If $R_0 > 1$ and $1 - \frac{\sqrt{2}}{2} \leq s < 1$ then there is a unique positive equilibrium, and this carrying capacity is stable.

(3) If $R_0 > 1$ and $0 < s < 1 - \frac{\sqrt{2}}{2}$ then there is a unique positive equilibrium. This carrying capacity equilibrium is stable if and only if $c \leq \frac{(1-s)^2}{2s^2 - 4s + 1}$.

Proof: The model (4.1) is equivalent to the following through the change of variables and parameters given by $N_0 \rightarrow \beta p_0 p_1 N_0, N_1 \rightarrow \beta p_1 N_1, N_2 \rightarrow \beta N_2$, and $m \rightarrow p_0 p_1 m$.

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ N_2(t+1) \end{bmatrix} = \begin{bmatrix} 0 & 0 & ms \\ 1 & 0 & 0 \\ 1 + N_2(t) & 0 & 0 \\ 0 & 1 & s \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ N_2(t) \end{bmatrix}$$

In the same manner as for Theorem 2.1, it is easy to show that the population becomes extinct if $ms + s - 1 \leq 0$ and that if $ms + s - 1 > 0$ there is a unique positive equilibrium at

$$N_2 = \frac{ms + s - 1}{1 - s}, N_1 = ms + s - 1, N_0 = \frac{ms(ms + s - 1)}{1 - s}$$

It remains to consider the stability of this equilibrium. To do this we compute the Jacobian matrix at the equilibrium to obtain:

$$\begin{bmatrix} 0 & 0 & ms \\ \frac{1-s}{ms} & 0 & -(1-s)(ms + s - 1) \\ 0 & 1 & s \end{bmatrix},$$

a matrix with one negative entry whose characteristic equation is given by

$$h(\lambda) = -\lambda^3 + s\lambda^2 - \frac{(1-s)(ms + s - 1)}{ms}\lambda + (1-s).$$

Since Perron-Frobenius theory does not apply, we use the Jury conditions (see, for example, Murray [10]) to determine stability. A lengthy calculation shows that the carrying capacity is stable if and only if

$$ms [2s^2 - 4s + 1] < (1-s)^2$$

If the expression $2s^2 - 4s + 1 < 0$, which is true for $1 - \frac{\sqrt{2}}{2} < s < 1$, then this is an identity, but if

$0 < s < 1 - \frac{\sqrt{2}}{2}$, this gives $ms < \frac{(1-s)^2}{2s^2 - 4s + 1}$ as the condition for stability.

To return to the original parameters, we replace m by $p_0 p_1 m$ so that the left-hand side becomes $m p_0 p_1 s = c$. Numerical work indicates that the carrying capacity equilibrium is globally asymptotically stable when it is stable and that a discrete Hopf bifurcation (sometimes called

Neimark-Sacker bifurcation) takes place on the curve $c = \frac{(1-s)^2}{2s^2 - 4s + 1}$. The Theorem is summarized in the bifurcation diagram shown in Fig. 2.

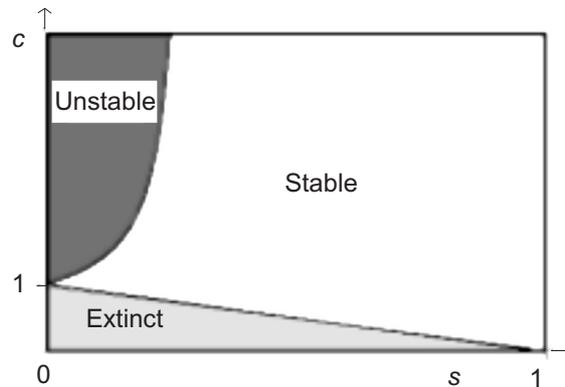


Fig. 2 Bifurcation diagram for the model (4.1). A flip transcritical bifurcation occurs on the linear boundary; numerical work indicates that a discrete Hopf (Neimark-Sacker) bifurcation takes place on the non-linear boundary.

5. BREEDING SUCCESS WITH SUBADULTS TREATED DIFFERENTLY TO ADULTS

In this section we consider the scenario of Section 3 in the more general setting of model (1.1). With fecundities f_{k+1} and m having the form (1.3), a rescaling of variables leads to the following model:

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ \dots \\ N_{k-1}(t+1) \\ N_{\bar{A}}(t+1) \end{bmatrix} = \begin{bmatrix} 0 & \dots & 0 & \frac{c_1}{1+N_{\bar{A}}(t)} & \frac{c_2 s}{1+N_{\bar{A}}(t)} \\ 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & 0 & 0 \\ 0 & \dots & 0 & 1 & s \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ \dots \\ N_{k-1}(t) \\ N_{\bar{A}}(t) \end{bmatrix} \tag{7}$$

Analysis of this model is much more difficult than the model considered in Section 3. In the case where $c_1 = c_2$, it is easy to show that the condition for a positive equilibrium is given by $c + s > 1$, and that the unique carrying capacity lies at

$$N_0 = N_1 = \dots = N_{k+1} = (c + s - 1); N_{\bar{A}} = \frac{(c + s - 1)}{1 - s},$$

but evaluation of the Jacobian matrix at carrying capacity yields a matrix that includes a negative term and as with the model considered in Section 4, the Perron-Frobenius theorem does not apply. Instead all roots of the characteristic equation must be considered to establish stability. Before considering some special cases, we state a general theorem about model (7):

Theorem 5.1: If $s = 0$, the model (5.1) has a stable k -cycle if and only if $c_1 > 1$.

Proof: Noting that the sizes of age-classes N_{k-1} and $N_{\bar{A}}$ are equal, and ignoring the latter age class which consists of post-breeding individuals gives the semelparous model (see for example, Mjølhus, Wikan and Solberg [11]):

$$\begin{bmatrix} N_0(t+1) \\ N_1(t+1) \\ \dots \\ N_{k-2}(t+1) \\ N_{k-1}(t+1) \end{bmatrix} = \begin{bmatrix} 0 & \dots & 0 & 0 & \frac{c_1}{1+N_{k-1}(t)} \\ 1 & \dots & 0 & 0 & 0 \\ \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & 1 & 0 & 0 \\ 0 & \dots & 0 & 1 & 0 \end{bmatrix} \begin{bmatrix} N_0(t) \\ N_1(t) \\ \dots \\ N_{k-2}(t) \\ N_{k-1}(t) \end{bmatrix}$$

It is easy to show that for $c_1 > 1$, there is a stable k -cycle given by $(c_1 - 1, 0, 0 \dots 0) \rightarrow (0, c_1 - 1, 0, 0 \dots 0) \rightarrow \dots \rightarrow (0, 0 \dots c_1 - 1, 0) \rightarrow (0, 0 \dots 0, c_1 - 1)$. This follows because this matrix equation can be rewritten as the delay difference equation

$$N_{k-1}(t+1) = \frac{c_1 N_{k-1}(t-k-1)}{1 + N_{k-1}(t-k-1)}$$

This has the form of the discrete logistic equation for which the carrying capacity is globally attracting.

Although a sub-adult/adult model does not apply when $s = 0$ (adults do not breed on an annual basis, only when they transition from sub-adults), this case is helpful in understanding the complex dynamics of the general model (5.1). Below we discuss the three simplest cases: $k = 2, 3$ and 4 . Specifically we work with the case $c_1 = c_2$ although some numerical work indicates little qualitative difference if these values are unequal.

The case $k = 2$: In this case, the Jury conditions can be used to determine the stability of the carrying capacity. In the case where $c_1 = c_2$, this condition requires $s < 1/3$ and is given by $c \leq \frac{(s-1)^2}{1-3s}$. A flip

bifurcation takes place across this curve, so that a stable 2-cycle replaces the stable carrying capacity. Also, in light of Theorem 5.1, there is a stable 2-cycle when $s = 0$. Numerical work

indicates that this stable 2-cycle persists throughout the region given by $0 \leq s < \frac{1}{3}, c > \frac{(s-1)^2}{1-3s}$. See

Fig. 5.1.

Numerical work indicates a similar qualitative diagram in the case where c_1 and c_2 are unequal. Again, solutions in the unstable region appear to tend to a stable 2-cycle.

The cases $k = 3$ and $k = 4$: In these cases, the Jury conditions are prohibitively difficult to apply, but numerically these cases have the same qualitative bifurcation diagram as Figure 3. (The equation of the boundary on which the carrying capacity loses stability will be different.)

In the $k = 3$ case, numerical work indicates that the carrying capacity loses stability through a discrete Hopf (Neimark-Sacker) bifurcation. Dynamics on what is initially a closed curve, settles down to a 3-cycle through the process known as phase locking. (This is similar to what happens in the model of Wikan and Mjølhus [7]). See Fig. 4.

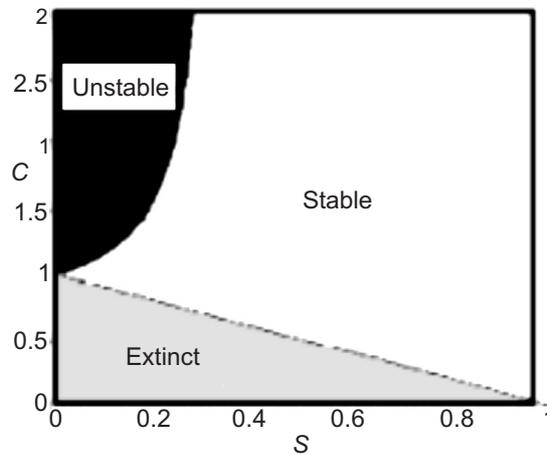


Fig. 3 Numerical bifurcation diagram for the model (5.1) with $k = 2$ and $c_1 = c_2$. A flip bifurcation occurs on the line $c = 1 - s$ and a period-doubling bifurcation occurs on $0 \leq s < \frac{1}{3}, c > \frac{(s-1)^2}{1-3s}$.

The blue region has a stable 2-cycle.

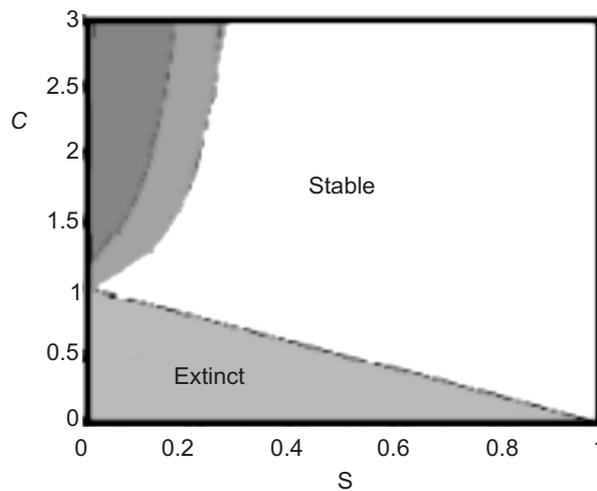


Fig. 4 Numerical bifurcation diagram for the model (5.1) when $k = 3$ and $c_1 = c_2$. A flip bifurcation occurs on the linear boundary; a discrete Hopf bifurcation occurs on the boundary between the white and blue regions. Phase locking occurs between the blue and brown. The brown region has a stable 3-cycle.

In the $k = 4$ case, numerical work indicates that the carrying capacity loses stability through a flip bifurcation to a stable 2-cycle. Although there is a stable 4-cycle on $s = 0$, the transition is not as simple as having a second flip bifurcation from a 2-cycle to a 4-cycle.

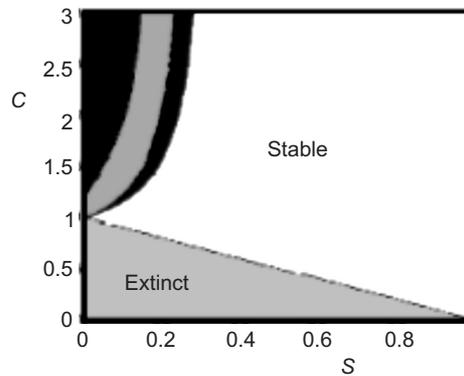


Fig. 5 Numerical bifurcation diagram for the model (5.1) when $k = 4$ and $c_1 = c_2$. A flip bifurcation occurs on the linear boundary; a period-doubling bifurcation occurs on the boundary between the white and red regions. The red region has a stable 2-cycle and the green region has a stable 4-cycle. There are no low order cycles in the blue region.

Numerical work in the case where $s = 0.15$ and $c_1 = c_2$ is incrementally increased indicates the initial 2-cycle period doubles to a 4-cycle which then loses stability. Following a *discrete Hopf* (*Neimark-Sacker*) bifurcation, phase locking returns this to a 4-cycle. See Fig. 5.

More work is required to fully understand model (5.1). It is clear from Theorem 5.1, that each value of k will have a different bifurcation diagram than for other values. Consideration of the cases $k = 2, 3$ and 4 indicate some of this diversity.

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