



Feedback control systems analysis of density dependent population dynamics

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ABSTRACT

We use feedback control methods to prove a trichotomy of stability for nonlinear (density dependent) discrete-time population dynamics defined on a natural state space of non-negative vectors. Specifically, using comparison results and small gain techniques we obtain a computable formula for parameter ranges when one of the following must hold: there is a positive, globally asymptotically stable equilibrium; zero is globally asymptotically stable or all solutions with non-zero initial conditions diverge. We apply our results to a model for Chinook Salmon.

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1. Introduction

The familiar feedback control design for single-input, single-output discrete-time systems

$$x_{t+1} = Ax_t + bu_t, \quad y_t = c^T x_t,$$

with nonlinear output feedback $u = f(y)$, leads to a closed-loop system

$$x_{t+1} = Ax_t + bf(c^T x_t). \quad (1.1)$$

Feedback descriptions of this type arise also in nonlinear population dynamics. For example, the population dynamics of a fish species (e.g., p. 316–323, [1]), with density dependent survival of eggs, can be modelled in this form. In this application, the state x_t describes the population structure of the fish at time t , with population structure determined by discrete, developmental-based stage classes. The right hand side of (1.1) captures two fundamental biological processes—survival/growth and fecundity of fish in each size class. In the case of (1.1), A models linear demographic transition rates, whilst the term $bf(c^T x_t)$ picks up specific nonlinear, density limited transitions. The matrix A is nonnegative (all entries of A are non-negative), $c^T x_t$ is a non-negative weighted population density and the non-negative vector

b describes the population structure of new-born fish. Density dependence is captured by f , which determines the nonlinear relationship between egg production and survival to one-year old fish.

Similar nonlinear (i.e. density dependent) models arise when considering the population dynamics of monocarpic plants, for example Platte Thistle, see Rose et al. [2]. In this case, the nonlinearity captures the density dependence of seedling establishment.

Typical density dependences which are used in population dynamic models are:

$$f(y) = \beta y^\alpha \quad \text{with } \alpha \in (0, 1) \text{ and } \beta > 0;$$

$$f(y) = \frac{Vy}{K + y} \quad \text{with } V > 0 \text{ and } K > 0;$$

$$f(y) = y \exp(-\beta y), \quad \beta > 0.$$

The first is a power-law type nonlinearity, the second is of the so-called Beverton–Holt (equivalently Michaelis–Menten) type [1] and the third is a Ricker nonlinearity, [3]. In the first two cases the nonlinearity f is monotone, but the third is not and $f(y)$ has a maximum.

Hence the nonlinear model (1.1) is a candidate for density dependent population dynamics of both flora and fauna. Whilst the feedback structure (1.1), is quite familiar in systems theory, this feedback structure has not been widely exploited in population biology.

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The paper is organised as follows: In Section 2 we formulate the assumptions about system (1.1) and state our main result, namely [Theorem 2.1](#). Section 3 is devoted to a proof of this main result via a sequence of lemmas. This section also contains an extension of this main result to the case when the underlying system is not monotone. In Section 4 we illustrate our main results with two examples.

2. Preliminaries and systems assumptions

We say that a vector or matrix is *nonzero* if at least one of its entries is nonzero, and a vector or matrix is *non-negative* if every entry is non-negative. Let $r(A)$ be the spectral radius of a matrix A . The following assumptions are used throughout:

- (A1) A is non-negative and $r(A) < 1$;
- (A2) the vectors b and c are non-negative and non-zero;
- (A3) the density dependence f is non-negative and continuous on $\{y \geq 0\}$, $f(0) = 0$ and

$$g(y) := f(y)/y$$
 is non-increasing for $y > 0$;
- (A4) $A + pbc^T$ is primitive for some $p \geq 0$, i.e. $(A + pbc^T)^k$ is a positive matrix for some $p \geq 0$ and $k \in \mathbb{N}$. Since the di-graph of $A + pbc^T$ is the same for all positive p , it follows that $A + pbc^T$ is, in fact, primitive for all non-negative p .

We associate with the linear system (A, b, c^T) the reciprocal of the steady state gain

$$p_e^* = \frac{1}{c^T(I - A)^{-1}b},$$

(which is finite and positive because of the assumed primitivity and that b and c are non-zero, see [Lemma 3.1](#)), and with the nonlinearity f the “nonlinear gains”

$$g_0 = \lim_{y \rightarrow 0^+} g(y) \in (0, \infty] \quad \text{and} \quad g_\infty = \lim_{y \rightarrow \infty} g(y) \in [0, g_0).$$

We say that an equilibrium x^* of (1.1) is *globally asymptotically stable* if $x_t \rightarrow x^*$ for every $x_0 \geq 0$. We show that the global dynamics of (1.1) exhibit a trichotomy which is completely characterised in terms of the steady state gain, or its reciprocal p_e^* , and the quantities g_0 and g_∞ equivalently, by the relationship between the graph of $f(y)$ and the line with slope p_e^* . In particular, the following theorem gives conditions under which 0 is a globally asymptotically stable equilibrium of (1.1), and conditions under which there exists a positive globally asymptotically stable equilibrium of (1.1).

Theorem 2.1. *Consider the nonlinear (density dependent) system (1.1). Under assumptions A1–A4, the following trichotomy of stability holds:*

1. If $g_0 < p_e^*$, then 0 is a globally asymptotically stable equilibrium of (1.1).
2. If $g_\infty > p_e^*$, then 0 is unstable and if x_0 is non-negative and non-zero, then x_t is strongly divergent so that

$$\lim_{t \rightarrow \infty} (\min(x_t)) = \infty \quad \text{for all non-negative } x_0.$$

3. Suppose in addition that f is non-decreasing on \mathbb{R}^+ . If $g_\infty < p_e^* < g_0$, then there exists $y^* > 0$ so that

$$f(y^*) = p_e^* y^*$$

and for all $x_0 \in \mathbb{R}_+^n$

$$\lim_{t \rightarrow \infty} x_t = x^*, \tag{2.1}$$

where the limit x^* is given by

$$x^* := (I - A)^{-1} b p_e^* y^*.$$

There is a vast literature on global stability of continuous-time and discrete-time population systems, but to our knowledge the nonlinear feedback structure of the model has not been exploited in the way we describe here. In Cushing’s survey lectures [4], a matrix model is decomposed into its survival and fertility matrices, although no decomposition of the fertility is used, nor do they obtain global asymptotic stability results of the type in this paper. The work most closely related to [Theorem 2.1](#) is work by Krause and Ranft [5], where a trichotomy of stability results are given for a general class of monotone systems satisfying a (k, P) property. In comparing the results in [5] and ours: The results in [5] are essentially existence proofs while our result is constructive and we can characterise the trichotomy via computable formulas which have meaningful biological interpretations; the (k, P) property required in [5] is difficult to verify—this will be especially the case when the density dependence is itself only approximated from data; finally, we can extend our result very easily to important cases where the system is not monotone.

Our feedback systems approach to analysing density dependent population models is inspired by small gain theorems from nonlinear feedback control theory and is, in essence, a case when Aizermann’s conjecture holds, see Hinrichsen and Pritchard [6]. This development of feedback systems techniques for density dependent population models compliments our previous feedback systems analysis of linear population projection matrix models, Lubben et al. [7] and fits within our long-term goal of promoting the development and use of feedback systems analysis approaches for population dynamics.

3. Proof of Theorem 2.1

To prove this result we combine a small-gain argument with a number of comparison-type arguments which are made possible because the dynamics (1.1) evolve on the cone \mathbb{R}_+^n of non-negative vectors—recall in particular that A, b, c are all non-negative and b and c are non-zero, and the f is non-negative. First we present some preliminary lemmas.

Lemma 3.1. *Assume that (A2) and (A4) hold. Then $c^T A^j b > 0$ for some j and*

$$G(\lambda) := c^T(\lambda I - A)^{-1}b > 0, \quad \text{for all } \lambda > r(A).$$

In particular $G(1) > 0$ (and hence $p_e^ < \infty$). Moreover, $G(\lambda)$ is a strictly decreasing function of λ , for $\lambda > r(A)$.*

Proof. Since $c^T A^j b \geq 0$ for all j , it is sufficient to prove that $c^T A^j b \neq 0$ for some j . Suppose that $c^T A^j b = 0$ for all j . Now $A + pbc^T$ is primitive, so that $(A + pbc^T)^k > 0$ for some k , and b and c are non-zero and non-negative. Then

$$0 < c^T(A + pbc^T)^k b = c^T$$

(positive linear combination of powers of A) b .

But $c^T A^j b = 0$ for all j , which is a contradiction. If $\lambda > r(A)$, then

$$c^T(\lambda I - A)^{-1}b = \frac{1}{\lambda} c^T \left(I + \frac{A}{\lambda} + \frac{A^2}{\lambda^2} \dots \right) b > 0.$$

Also, if $\mu > \lambda > r(A)$, then

$$\begin{aligned} G(\mu) &= \frac{1}{\mu} c^T \left(I + \frac{A}{\mu} + \frac{A^2}{\mu^2} \dots \right) b \\ &< \frac{1}{\lambda} c^T \left(I + \frac{A}{\lambda} + \frac{A^2}{\lambda^2} \dots \right) b. \quad \square \end{aligned}$$

Lemma 3.2. *If $p = p_e^*$, then $r(A + pbc^T) = 1$. Moreover, if $p < p_e^*$, then $r(A + pbc^T) < 1$, whilst if $p > p_e^*$, then $r(A + pbc^T) > 1$. Furthermore, in all cases, the primitivity assumption guarantees that the corresponding left and right eigenvectors v^T and w are positive.*

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