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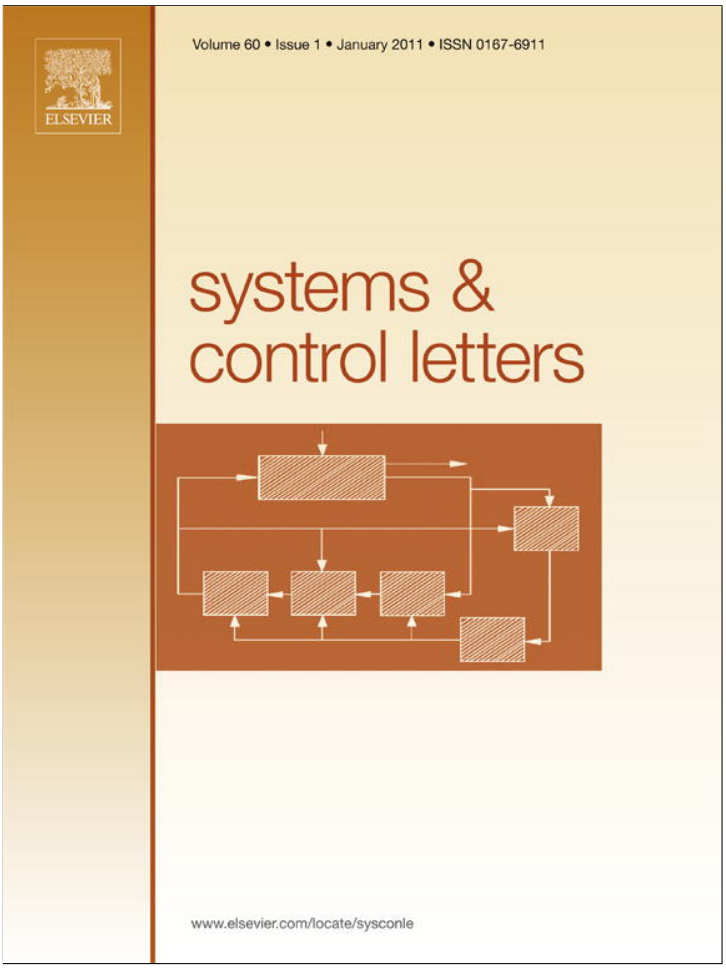

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Systems & Control Letters 61 (2012) 309–315

Contents lists available at SciVerse ScienceDirect

Systems & Control Letters

journal homepage: www.elsevier.com/locate/sysconle

Feedback control systems analysis of density dependent population dynamics

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ARTICLE INFO

Article history:
Received 27 May 2011
Received in revised form
22 November 2011
Accepted 26 November 2011

Keywords:
Beverton–Holt function
Density dependence
Feedback
Population dynamics
Ricker function
Small gain

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

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

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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doi:10.1016/j.sysconle.2011.11.014

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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 in 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"

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

We say that an equilibrium x^* of (1.1) is *globally asymptotically stable* if $x_t \to x^*$ 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*

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

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

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

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 in 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*

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

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

$$0 < c^T(A + pbc^T)^k b = c^T$$
$$\text{(positive linear combination of powers of } A)b.$$

But $c^T A^j b = 0$ for all j, which is a contradiction.

If $\lambda > r(A)$, then

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

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

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

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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Proof. We know that $G(\lambda) > 0$, for all $\lambda > r(A)$. In particular $G(1) = c^T(I-A)^{-1}b > 0$. Now

$$(A + p_e^* bc^T)(I-A)^{-1}b = A(I-A)^{-1}b + b = (I-A)^{-1}b.$$

Hence $(I-A)^{-1}b$ is a non-negative eigenvector of $A + p_e^* bc^T$, corresponding to the eigenvalue one. Then $(A + p_e^* bc^T)^k (I-A)^{-1}b$ is a positive eigenvector of the primitive $A + p_e^* bc^T$. So by the Perron–Frobenius Theorem, $r(A + p_e^* bc^T) = 1$.

If $p < p_e^*$, then $A + pbc^T \le A + p_e^* bc^T$ and so $r(A + pbc^T) \le r(A + p_e^* bc^T) = 1$. But $\lambda = 1$ cannot be an eigenvalue of $(A + pbc^T)$ because if it were

$$\frac{1}{G(1)} = p < p_e^* = \frac{1}{G(1)},$$

a contradiction.

Similar arguments apply when $p > p_e^*$. □

Proof of Theorem 2.1, Part 1. We need to show that if $g_0 < p_e^*$, then $x = 0$ is globally asymptotically stable.

If $g_0 < p_e^*$, then

$$x_{t+1} = Ax_t + bf(c^T x_t) = Ax_t + bg(c^T x_t)c^T x_t \le Ax_t + pbc^T x_t$$

for some $p < p_e^*$. Then

$$\|x_t\| \le \|(A + pbc^T)^t x_0\|.$$

The result now follows because $r(A + pbc^T) < 1$. □

Proof of Theorem 2.1, Part 2. We need to show that if $g_\infty > p_e^*$, then $x = 0$ is unstable and if $x_0 \ge 0$ and non-zero, then $\lim_{t\to\infty} \min(x_t) = \infty$.

If $g_\infty > p_e^*$, then

$$x_{t+1} = Ax_t + bf(c^T x_t) \ge Ax_t + pbc^T x_t \tag{3.1}$$

for some $p > p_e^*$. Let v^T and w be the positive left and right eigenvectors of $A + pbc^T$ corresponding to the dominant eigenvalue $\lambda = r(A + pbc^T) > 1$. Then, using an eigenmode expansion in the right hand side of the inequality (3.1),

$$\lim_{t\to\infty} \lambda^{-t} x_t \ge \lim_{t\to\infty} \lambda^{-t}(A + pbc^T)^t x_0 = \frac{v^T x_0}{v^T w} w,$$

and the result now follows from positivity of v and w and the fact that x_0 is non-negative and non-zero. □

Proof of Theorem 2.1, Part 3. We break the proof of this part of the theorem into a number of lemmas. First we note that because $g_\infty < p_e^* < g_0$, then there exists y^* so that

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

which in turn defines the candidate non-negative equilibrium x^* by

$$x^* = (I-A)^{-1} p_e^* by^*. \quad \square \tag{3.2}$$

Lemma 3.3. *For each $R > 0$, there exists $M > 0$, so that if $\|x_0\| \le R$, then $\|x_t\| \le M$ and $y_t \le \|c^T\| M$ for all $t \ge 0$.*

Proof. Since $g_\infty < p_e^* < g_0$, we know that for all large enough positive y, $g(y) \le m$ (hence $f(y) \le my$) for some $m < p_e^*$. On the other hand, $f(y)$ is continuous and therefore bounded on any bounded interval in $\mathbb{R}^+$. Therefore, there exists $\hat{f}$ so that

$$f(y) \le \hat{f} + my, \quad \text{for all } y \ge 0.$$

Now fix x_0 with $\|x_0\| \le R$. Then

$$x_{t+1} = Ax_t + bf(c^T x_t) \le Ax_t + b\hat{f} + mbc^T x_t = (A + mbc^T)x_t + b\hat{f}.$$

The spectral radius of $(A + mbc^T)$ is less than one. Hence for all $R > 0$, there exists M so that $\|x_t\| \le M$ for all $\|x_0\| \le R$. So when x_0 is in a ball, x_t is bounded and $y_t = c^T x_t$ is too. □

Lemma 3.4. *Let v^T be the positive left eigenvector of $A + p_e^* bc^T$. For all x_0, the solution x_t satisfies*

$$v^T x_t \ge \min\left\{v^T x_0, v^T bp_e^* y^*\right\} > 0 \quad \textit{for all } t \ge 0 \tag{3.3}$$

and

$$\|x_t\|_1 \ge \frac{1}{\|v\|_\infty} v^T x_t. \tag{3.4}$$

Proof. Multiplying (1.1) on the left by v^T we obtain

$$v^T x_{t+1} = v^T Ax_t + v^T bf(y_t).$$

If $y_t \le y^*$, then $f(y_t) \ge p_e^* y_t$, and so

$$v^T x_{t+1} \ge v^T Ax_t + v^T bp_e^* y_t = v^T(A + p_e^* bc^T)x_t = v^T x_t. \tag{3.5}$$

If $y_t > y^*$, then $f(y_t) \ge p_e^* y^*$, and so

$$v^T x_{t+1} \ge v^T Ax_t + v^T bp_e^* y^* \ge v^T bp_e^* y^*. \tag{3.6}$$

It follows that

$$v^T x_t \ge \min\left\{v^T x_0, v^T bp_e^* y^*\right\} \quad \text{for all } t \ge 0,$$

as required. The inequality (3.4) follows from

$$v^T x_t \le \|v\|_\infty \|x_t\|_1. \quad \square$$

Lemma 3.5. *For each nonzero, nonnegative $x_0 \ge 0$, y_t is bounded away from zero for all $t \ge k$ (here k is such that $(A + pbc^T)^k$ is positive) and*

$$|f(y_t) - f^*| \le m|y_t - y^*|, \quad \textit{for some } m < p_e^* \textit{ and all } t \ge k. \tag{3.7}$$

Proof. For a given x_0, we know

1. from Lemma 3.3 that y_t is bounded from above by $\bar{M} = \|c^T\| M$;
2. from Lemma 3.4 that $\|x_t\|$ is bounded uniformly away from 0.

Hence, we can be sure that

$$f(y_t) = g(y_t)y_t \ge \underline{g} y_t, \quad \text{with } \underline{g} \ge g(\bar{M}) > 0, \text{ and all } t \ge 0.$$

Then for all $t \ge k$

$$\begin{aligned} x_t &= (A + bg(y_{t-1})c^T)\, x_{t-1} \\ &\ge (A + b\underline{g}c^T)x_{t-1} \cdots \ge (A + b\underline{g}c^T)^k x_{t-k}. \end{aligned}$$

Since c is non-negative, $c^T(A + b\underline{g}c^T)^k$ is positive and $\|x_t\|$ is bounded uniformly away from 0. Hence

$$y_t = c^T x_t \ge c^T(A + b\underline{g}c^T)^k x_{t-k}$$

is bounded uniformly away from zero for all $t \ge k$. Now using the fact that f is non-decreasing, we can be sure that the sector condition

$$|f(y_t) - f^*| \le m|y_t - y^*|, \quad \text{for some } m < p_e^* \text{ and all } t \ge k$$

holds. □

We now prove Theorem 2.1, Part 3 by exploiting a small gain argument.

We see from (3.2) that $x^* = Ax^* + p_e^* by^* = Ax^* + p_e^* bf(y^*)$. Combining this with (1.1),

$$x_{t+1} - x^* = A(x_t - x^*) + p_e^* b(f(y_t) - f(y^*)).$$

From the variation of parameters formula, when $t \ge 1$,

$$x_{t+k} - x^* = A^t(x_k - x^*) + \sum_{j=0}^{t-1} A^{t-j-1} b(f(y_{k+j}) - f(y^*)). \tag{3.8}$$

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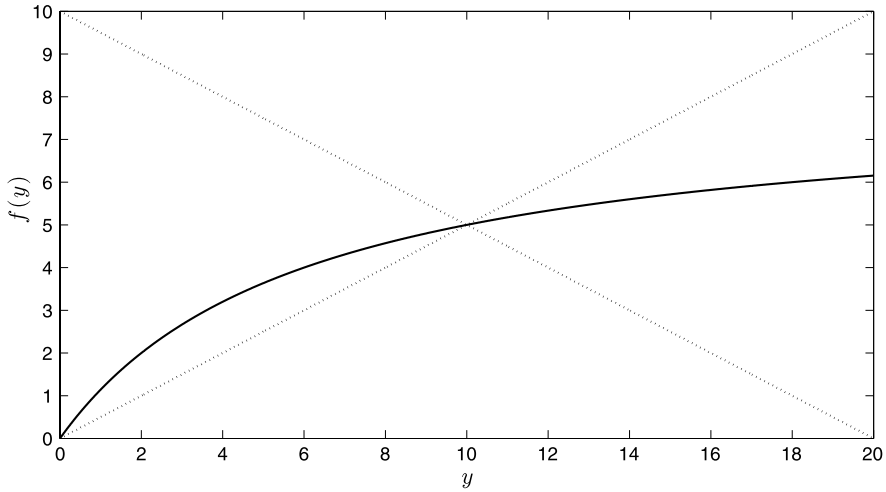

Fig. 3.1. Typical non-decreasing nonlinearity f (solid) and sectors defined by lines with slopes $\pm p_e^*$ (dotted) showing how (3.7) holds.

Multiplying (3.8) on the left by c^T and using the sector condition (3.7) (see Fig. 3.1) and the non-negativity of A, b, and c gives

$$|y_{t+k} - y^*| = \left| c^T A^t (x_k - x^*) + \sum_{j=0}^{t-1} c^T A^{t-j-1} b (f(y_{k+j}) - f(y^*)) \right|$$
$$\leq |c^T A^t (x_k - x^*)| + m \sum_{j=0}^{t-1} c^T A^{t-j-1} b |y_{k+j} - y^*|.$$

Hence,

$$\sum_{t=k}^{\infty} |y_t - y^*| \leq |c^T (x_k - x^*)| + \sum_{t=1}^{\infty} |c^T A^t (x_k - x^*)|$$
$$+ m \sum_{t=1}^{\infty} \sum_{j=0}^{t-1} c^T A^{t-j-1} b |y_{j+k} - y^*|.$$

Interchanging the order of summation and changing the summation variable in the last sum, gives

$$\sum_{t=k}^{\infty} |y_t - y^*| \leq \sum_{t=0}^{\infty} |c^T A^t (x_k - x^*)| + m \sum_{j=0}^{\infty} \sum_{i=0}^{\infty} c^T A^i b |y_{j+k} - y^*|.$$

Now

$$\sum_{i=0}^{\infty} c^T A^i b = c^T (I - A)^{-1} b = \frac{1}{p_e^*},$$

the steady state gain of the linear system (A, b, c^T). Hence

$$\sum_{t=k}^{\infty} |y_t - y^*| \leq \sum_{t=0}^{\infty} |c^T A^t (x_k - x^*)| + m c^T (I - A)^{-1} b \sum_{j=k}^{\infty} |y_j - y^*|,$$

so that

$$\sum_{t=k}^{\infty} |y_t - y^*| \leq (1 - m/p_e^*)^{-1} \sum_{t=0}^{\infty} |c^T A^t (x_k - x^*)|. \tag{3.9}$$

Using the facts that $m < p_e^*$ and $r(A) < 1$, we see that $\{|y_t - y^*|\}$ is l^1 and so $\lim_{t\to\infty} y_t = y^*$. It then follows from (3.7) and (3.8) that (2.1) holds. □

Inspecting the proof of Theorem 2.1, we can see that the assumptions on the nonlinearity f can be relaxed quite significantly. In particular, we do not need monotonicity of the system, as required in [5]. This is important for applications where it is possible that f has a maximum value.

Our proof relies on the existence of a unique y^* so that

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

and that $f(y)$ is sector bounded after moving the origin from $(0, 0)$ to (y^*, f^*) in the sense that

$$|f(y) - f^*| \leq m|y - y^*|, \quad \text{for some } m < p_e^*,$$

see Fig. 3.2. Clearly, we do not need f to be increasing (in particular, we do not need the system to be monotone) and convex for this to hold. Indeed, the function

$$f(y) = y \exp(-\beta y), \qquad g(y) = \exp(-\beta y)$$

(where f is called a Ricker function) satisfies these extended conditions if $p_e^* \in (\exp(-2), 1)$.

To see this, observe that for this Ricker function $f(y) = y \exp(-\beta y)$, we have

$$f'(y) = \exp(-\beta y)(1 - \beta y) \quad \text{and}$$
$$f''(y) = -\beta \exp(-\beta y)(2 - \beta y)$$

Hence $f'' \leq 0$ on $[0, 2/\beta]$ and so f is concave down on $[0, 2/\beta]$. On $(0, 1/\beta) f'$ is positive and decreasing. On $(1/\beta, 2/\beta)$ f' is negative and decreasing. On $[2/\beta, \infty)$, f' is negative and non-decreasing.

Since $f(y) = y \exp(-\beta y) \leq y$ for all $y \geq 0$, it follows from the proof of Theorem 2.1, Part 1 that if $p_e^* > 1$, then 0 is globally asymptotically stable.

If $p_e^* < 1$, then the nonlinearity $f(y)$ intersects the line with slope p_e^* at $y = y^*$ when

$$\exp(-\beta y^*) = p_e^*.$$

If $e^{-2} < p_e^* < 1$, then $y^* < 2/\beta$. Using the convexity of f on $[0, 2/\beta]$ and the fact that f' is negative and decreasing on $[1/\beta, 2/\beta)$ and non-decreasing on $[2/\beta, \infty)$ it follows that

$$|f(y) - f^*| \leq m|y - y^*|, \quad \text{for some } m < p_e^* \text{ and all } y \geq 0.$$

However, when $p_e^* < e^{-2}$, then $y^* > 2/\beta$ and

$$f'(y^*) = p_e^*(1 - \beta y^*) = p_e^*(1 + \log(p_e^*)) < -p_e^*.$$

In this case the sector condition fails. However, $f(y) = y \exp(-\beta y)$ is bounded on $[0, \infty)$. Therefore, since $r(A) < 1$, then trajectories are always bounded.

We will return to this nonlinearity f in Section 4.

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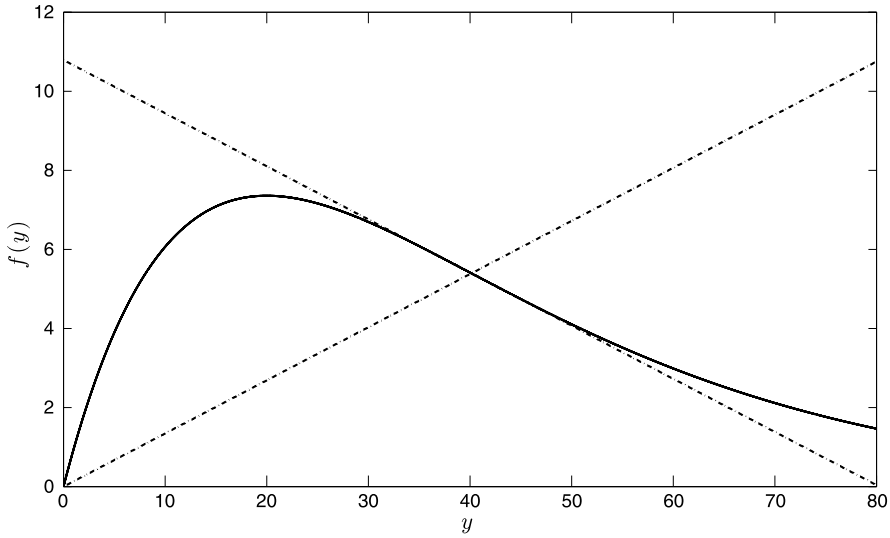

Fig. 3.2. Ricker function (solid) trapped by sectors defined by lines (dash–dotted) with slope $\pm p_e^*$, $p_e^* \in (e^{-2}, 1)$.

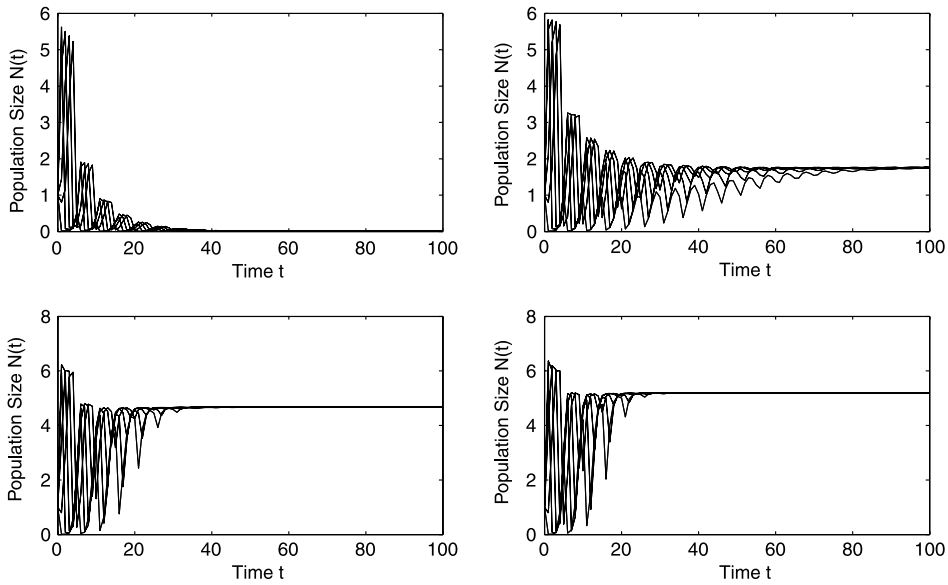

Fig. 4.3. Simulations of the global dynamics with Beverton–Holt nonlinearity. As p_e^* decreases we move from 0 being globally asymptotically stable (the upper left graph), to the existence of a positive, globally asymptotically stable steady state in the other graphs.

4. Example

We consider a simple population projection matrix model for Chinook Salmon. First we assume a Beverton–Holt type survival function. Second, we extend our analysis to a Ricker-type density dependence.

Example 4.1. The model is structured with 5 stage classes with stages 3–5 representing adult fish which spawn. We assume a population projection matrix in the form

$$A = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 \\ s_1 & 0 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 & 0 \\ 0 & 0 & s_3 & 0 & 0 \\ 0 & 0 & 0 & s_4 & 0 \end{pmatrix} \qquad b = \begin{pmatrix} 1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix} \qquad c = \begin{pmatrix} 0 \\ 0 \\ f_3 \\ f_4 \\ f_5 \end{pmatrix}.$$

In this case $A + pbc^T$ is primitive for all positive p and the smallest power so that $(A + pbc^T)^k$ is a positive matrix is $k = 8$.

We have

$$c^T(I - A)^{-1}b = f_3 s_1 s_2 + f_4 s_1 s_2 s_3 + f_5 s_1 s_2 s_3 s_4 = R,$$

the reproductive rate of the population. Hence, in this case we have

$$p_e^* = \frac{1}{c^T(I - A)^{-1}b} = \frac{1}{f_3 s_1 s_2 + f_4 s_1 s_2 s_3 + f_5 s_1 s_2 s_3 s_4} = \frac{1}{R}.$$

In the simulations we adopt parameter values

$$s_1 = 0.0131, \qquad s_2 = 0.8, \qquad s_3 = 0.7896, \qquad s_4 = 0.6728$$

and choose four values of $c^T = rc_0^T$ with

$$c_0^T = [0\ 0\ 0.3262\ 5.0157\ 39.6647], \quad \text{and} \quad r = 3,\ 7,\ 20,\ 30.$$

This gives values of

$$R = 0.7973,\ 1.8603,\ 5.3151 \text{ and } 7.9726$$

and

$$p_e^* = 1.2543,\ 0.5376,\ 0.1881 \text{ and } 0.1254 \text{ respectively.}$$

Suppose in the first case, a Beverton–Holt type nonlinearity

$$f(y) = \frac{Vy}{K + y}, \quad \text{for positive constants } V \text{ and } K.$$

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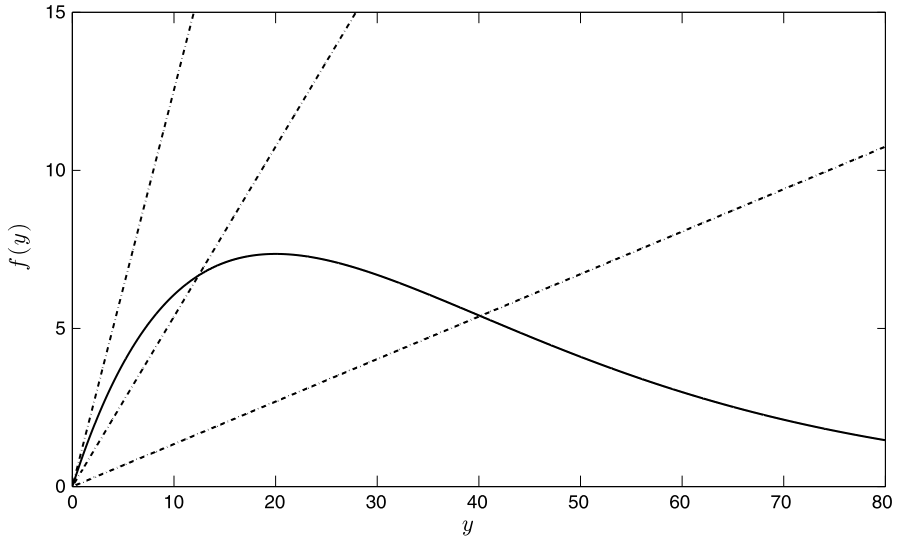

Fig. 4.4. The Ricker function and lines with slope (from left to right) $p_e^* = 1/R$ with $p_e^* > 1$, $p_e^* \in (e^{-2}, 1)$ and $p_e^* < e^{-2}$.

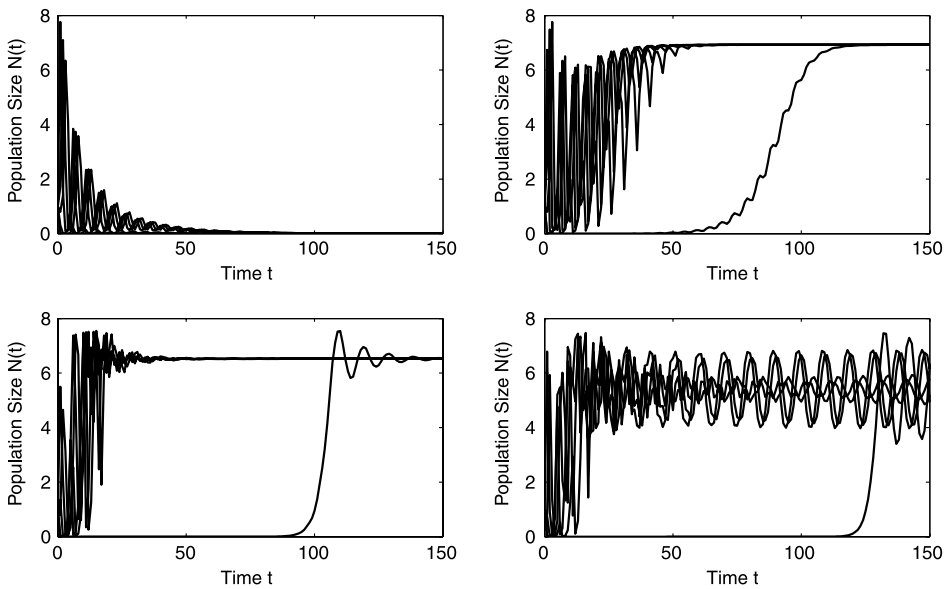

Fig. 4.5. Simulations of the global dynamics with decreasing $p_e^* = 1/R$ showing that when $p_e^* > 1$, $x = 0$ is globally asymptotically stable (upper left); for $p_e^* \in (e^{-2}, 1)$, there is a positive globally asymptotically stable equilibrium (upper right and lower left); but when $p_e^* < e^{-2}$, the positive steady state becomes unstable but solutions remain bounded (lower right). In each case we choose five different initial conditions biased totally to each of the five stage classes, i.e. $x_0 = e_i$, $i = 1, \ldots, 5$.

Then

$$g_0 = \frac{V}{K} \quad \text{whilst } g_\infty = 0.$$

Hence in this case,

1. 0 is globally asymptotically stable if $RV < K$ and
2. there is a positive, globally asymptotically stable equilibrium if $RV > K$.

We can see from this example how computable conditions for the trichotomy translate to specific criteria in terms of systems data.

In the simulations in Fig. 4.3, we take values $V = 6$ and $K = 8$ so that $g_0 = 3/4$.

Suppose that we use instead a Ricker-type nonlinearity

$$f(y) = y \exp(-\beta y).$$

In this case, $f(y)$ has a maximum and it is neither convex nor increasing, so the results in [5] do not apply. However, when p_e^* is in the range between e^{-2} and 1, then as discussed above we have the sector condition

$$|f(y) - f^*| \le m|y - y^*|$$

for some $m < p_e^*$, see also Fig. 4.4. Hence,

1. If $Re^{-2} < 1 < R$, there is a positive globally stable equilibrium x^*;
2. If $R < 1$, then $x = 0$ is globally asymptotically stable;
3. If $Re^{-2} > 1$, then $x = x^*$ need not be globally asymptotically stable, but all trajectories are bounded because $f(y)$ is.

In the simulations we use the value $\beta = 0.05$. For the four different values

$$p_e^* = 1.2543,\ 0.5376,\ 0.1881 \text{ and } 0.1254:$$

the first value gives $p_e^* > 1$, the second and third give $p_e^* \in (e^{-2}, 1)$ whilst for the fourth $p_e^* < e^{-2}$. The simulations in Fig. 4.5 confirm that for $p_e^* = 1.2543$, 0 is globally asymptotically stable, for $p_e^* =$

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0.5376 and $p_e^* = 0.1881$ there is a positive, globally asymptotically stable steady state whilst for $p_e^* = 0.1254$ the positive steady state is unstable, but all solutions are bounded.

This nonlinear feedback analysis of the Chinook Salmon model quantifies the qualitatively different behaviour of this model observed in [1].

Notice in this example, that an initial condition biased towards stage class 5, i.e. with $x_0 \approx [0\,0\,0\,0\,1]^T$, produces a large y_0 which because of the term $\exp(-\beta y_t)$ in the model, makes x_1 negligible. It then takes approximately 100 time steps for the population to become re-established.

5. Concluding remarks

We have used feedback control methods, specifically comparison results and small gain techniques, to characterise a trichotomy of stability for nonlinear (density dependent) population dynamics. We have focused on populations modelled in discrete size or stage classes where the natural state space is the cone of nonnegative vectors in $\mathbb{R}^n$. Our results do not require the system to be monotone and so our results generalise trichotomy of stability results in [5]. The characterisation of the trichotomy requires knowledge of a steady state gain $G(1)$ and sector-type constraints on f which will be checkable without precise knowledge of the system. Determining stability type from poor data is important in ecological applications because paucity of, and uncertainty in, data is the norm. We apply our results to a model of Chinook Salmon. In this case, ranges of parameters where the various limiting behaviours occur can be characterised by the population's reproductive rate. In Rebarber et al. [8], we give versions of our results for Integral Projection Models (see [9,10]) which are relevant for populations, such as plants, that are best described by continuous size structures.

Acknowledgment

Richard Rebarber was supported in part by NSF Grant 0606857.

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