Systems & Control Letters 65 (2014) 30–36

Contents lists available at ScienceDirect

Systems & Control Letters

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

Global stability of an age-structured population model

Daniel Franco [a,b,*], Hartmut Logemann [b], Juan Perán [a]

[a] Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED), c/ Juan del Rosal 12, 28040, Madrid, Spain

[b] Department of Mathematical Sciences, University of Bath, Bath BA2 7AY, UK

ARTICLE INFO

Article history:
Received 15 July 2013
Received in revised form
18 November 2013
Accepted 21 November 2013
Available online 22 January 2014

Keywords:
Age-structured species
Feedback systems
Global stability
Lure systems
Population dynamics

ABSTRACT

We consider a nonlinear discrete-time population model for the dynamics of an age-structured species. This model has the form of a Lure feedback system (well-known in control theory) and is a particular case of the system studied by Townley et al. in Townley et al. (2012). The main objective is to show that, in this case, the range of nonlinearities for which the existence of globally asymptotically stable non-zero equilibrium can be guaranteed is considerably larger than that in the main result in Townley et al. (2012). We illustrate our results with several biologically meaningful examples.

1. Introduction

Leslie matrix models have been widely employed to understand the dynamics of populations structured into age classes [1]. The model can be written as follows

$$x_{t+1} = P(x_t)x_t. \tag{1}$$

Here $x_t \in \mathbb{R}_+^n$ is the class distribution vector (where $\mathbb{R}_+ = [0, \infty)$) at discrete time $t \in \mathbb{N}$ and

$$P(x) = \begin{pmatrix} \rho + \phi_1(x) & \phi_2(x) & \phi_3(x) & \cdots & \phi_n(x) \\ \tau_1(x) & 0 & 0 & \cdots & 0 \\ 0 & \tau_2(x) & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & \tau_{n-1}(x) & 0 \end{pmatrix},$$

with $0 < \tau_i \le 1$ and $0 \le \phi_i$. The subdiagonal elements, τ_i, capture the demographic transitions between age-categories, whilst in the elements in the first row, ϕ_i correspond to the newborns and ρ is the fraction of individuals in the first age class who remain in this class after one time unit (for example, because they do not mature in one time step).

In this paper, we consider the following system

$$x_{t+1} = Ax_t + bf(c^T x_t), \tag{2}$$

where A is an asymptotically stable non-negative matrix in $\mathbb{R}^{n\times n}$, $b, c \in \mathbb{R}_+^n \setminus \{0\}$ and $f : \mathbb{R}_+ \to \mathbb{R}_+$ is a continuous map with $f(0) = 0$ and $f(y) > 0$ for $y \in \mathbb{R}_+ \setminus \{0\}$. Systems of the form (2) are known in systems & control theory as Lure systems, the stability properties of which have been studied in the context of the so-called absolute stability theory (mainly in a continuous-time setting); see, for example [2,3]. Introducing the linear controlled and observed system

$$x_{t+1} = Ax_t + bu_t, \qquad y_t = c^T x_t, \tag{3}$$

the Lure system (2) can be thought of as the closed-loop system obtained by applying nonlinear feedback of the form $u_t = f(y_t)$ to the linear system (3).

We note that if A and b satisfy

$$A = \begin{pmatrix} 1-\delta & 0 & 0 & \cdots & 0 \\ a_1 & 0 & 0 & \cdots & 0 \\ 0 & a_2 & 0 & \cdots & 0 \\ \vdots & \ddots & \ddots & \ddots & \vdots \\ 0 & \cdots & 0 & a_{n-1} & 0 \end{pmatrix}, \qquad b = \begin{pmatrix} b_1 \\ 0 \\ 0 \\ 0 \\ 0 \end{pmatrix},$$

$$\text{where } 0 < \delta \le 1, \text{ and } a_i, b_1 > 0, \tag{4}$$

then system (2) is a particular case of system (1) in which a constant proportion of the individuals in each age-category, from 1 to $n-1$, at time-step t reaches the next age class in the time-step $t+1$,

* Corresponding author at: Departamento de Matemática Aplicada, E.T.S.I. Industriales, Universidad Nacional de Educación a Distancia (UNED), c/ Juan del Rosal 12, 28040, Madrid, Spain. Tel.: +34 913988134.
E-mail address: dfranco@ind.uned.es (D. Franco).

0167-6911/$ – see front matter
http://dx.doi.org/10.1016/j.sysconle.2013.11.012

i.e., the functions $\tau_i(x) = a_i$ are constant; moreover, $\rho = 1 - \delta$ and $\phi_i(x) = b_1 f(c^T x)/\|x\|_1$ for all i, where $\|\cdot\|_1$ is the 1-norm in $\mathbb{R}^n$, that is, $\|x\|_1 = \sum_{i=1}^n |x_i|$, where x_i denotes the ith component of x.

The global dynamics of (2) have been recently considered in [4], where it is shown that (under certain conditions) system (2) satisfies a trichotomy of stability, which is characterised by the relationship between the graph of f and the line with slope

$$p := \frac{1}{c^T (I - A)^{-1} b}.$$

We emphasise that the results in [4] are not restricted to the special case given in (4). Nevertheless, in [4], those results are illustrated by a model for *Chinook Salmon* (*Oncorhynchus tshawytscha*) which satisfies (4).

In [4], the following sector property for f is crucial for the proof of the existence of a positive global attractor for system (2).

(C) There exists a unique $y^* > 0$ so that $f(y^*) = py^*$ and

$$|f(y) - py^*| < p|y - y^*|, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\}. \tag{5}$$

Actually, in [4], the stronger assumption that there exists $m \in (0, p)$ such that

$$|f(y) - py^*| \le m|y - y^*|, \quad y \in \mathbb{R}_+ \setminus \{0, y^*\} \tag{6}$$

was imposed. Although not explicitly stated in [4], (6) guarantees global exponential stability, whilst (5) is sufficient for global asymptotic stability.

Defining $f_p : \mathbb{R}_+ \to \mathbb{R}_+$ by

$$f_p(y) = f(y)/p, \quad y \in \mathbb{R}_+,$$

we remark that the sector condition (C) implies that y^* is a global attractor for the scalar difference equation

$$z_{t+1} = f_p(z_t), \tag{7}$$

where by global we mean that for all positive y, the orbit $f^n(y)$ of y converges to y^* as $n \to \infty$. Condition (C) is satisfied, for example, by the Beverton–Holt map ($f(y) = \lambda y/(K + y)$, $\lambda, K > 0$) and the Ricker map ($f(y) = y\exp(-\lambda y)$, $\lambda > 0$), whenever $|f'(y^*)| < p$, i.e. when the fixed point y^* of the map f_p is locally asymptotically stable: the proof for the Beverton–Holt map is straight-forward and the reader can find the Ricker map case discussed in [4]. However, as Fig. 1 illustrates, for other important maps, the condition $|f'(y^*)| < p$ is not sufficient for (C) to hold. For example, this happens in the case of the generalised Beverton–Holt map [5],

$$f(y) = \frac{\lambda y}{1 + (y/K)^\beta}, \quad K > 0,\ \lambda > 0,\ \beta > 0,$$

or the Hassel map [6],

$$f(y) = \frac{\lambda y}{(1 + y/K)^\beta}, \quad K > 0,\ \lambda > 0,\ \beta > 0.$$

Generalised Beverton–Holt (also called Maynard-Smith) and Hassel maps have been extensively employed in ecological modelling. Moreover, the corresponding dynamics are well known. Interestingly, these maps have the very desirable property, as have many others density dependences, that the corresponding global dynamics can be characterised by the local dynamics [7], i.e. local stability guarantees global stability. This naturally raises the question of whether or not condition (C) can be relaxed.

In this paper, we show that the sector condition (C) is not necessary to establish the existence of a positive global attractor for system (2) when A and b are given by (4). We prove that, in this case, it is sufficient that the scalar difference equation (7) has a positive global attractor y^*. This will allow us to use well-known sufficient conditions for global stability for maps to formulate easily verifiable conditions for the existence of a positive global attractor for system (2) with A and b as in (4). We illustrate this idea with two different conditions which involve Schwarzian derivatives and envelopments by linear fractional functions.

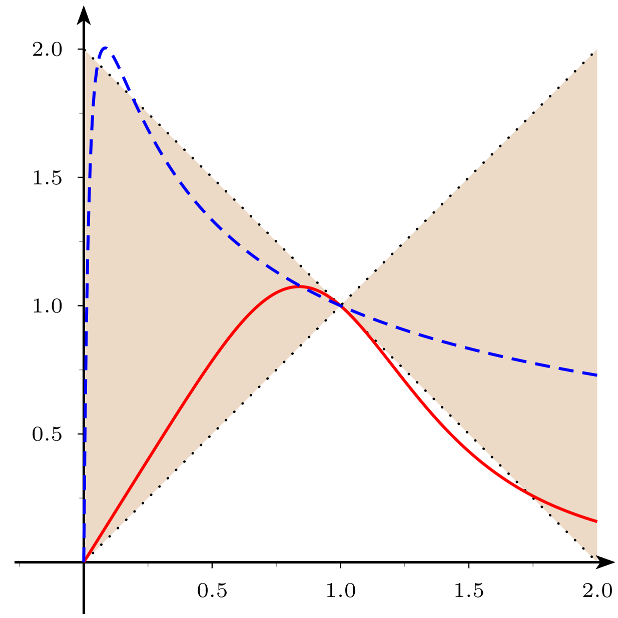

Fig. 1. The sector region, in the case $p = 1$, appears in light brown colour. Observe that condition (C) is not satisfied: neither by the generalised Beverton–Holt map with $K = \sqrt[5]{5/3}$, $\lambda = 8/5$, $\beta = 5$ (solid red curve) nor by the Hassel map with $K = 1/24$, $\lambda = 125$, $\beta = 3/2$ (dashed blue curve). For the chosen parameters $y^* = 1$ is the unique positive solution of the equation $f(y) = y$ and $|f'(1)| < 1$ for both maps.

Our approach is different from that in [4] which is essentially based on arguments of small-gain type. Indeed, small-gain and absolute stability arguments do not apply to the nonlinearities considered in this paper. Instead, we exploit that, in our particular case, system (2) can be reduced to an n-th order scalar difference equation with dynamics dominated by those of a first-order difference equation (see [8,9] and references therein).

2. Preliminaries

We start with some definitions. For a continuous map $F: \mathbb{R}^n_+ \to \mathbb{R}^n_+$, consider the difference equation

$$x_{t+1} = F(x_t), \quad t \ge 0, \tag{8}$$

with initial condition $x_0 \in \mathbb{R}^n_+$. We say that a non-zero equilibrium $x^* \in \mathbb{R}^n_+$ of Eq. (8) is a *global attractor* if, for every $x_0 \in \mathbb{R}^n_+ \setminus \{0\}$,

$$\lim_{k\to\infty} F^k(x_0) = x^*,$$

where, as usual, F^k denotes the k-fold composition of F with itself.

Similarly, for a continuous map $G: \mathbb{R}^n_+ \to \mathbb{R}_+$, consider the n-th order difference equation

$$y_{t+1} = G(y_t, y_{t-1} \dots, y_{t-n+1}), \quad t \ge 0, \tag{9}$$

with initial conditions $y_0, \dots, y_{1-n} \in \mathbb{R}_+$. We say that $y^* \in \mathbb{R}_+$ is an *equilibrium* of Eq. (9) if $y^* = G(y^*, \dots, y^*)$, and we say that such a non-zero equilibrium is a *global attractor* if

$$\lim_{k\to\infty} y_k = y^*,$$

for every solution $\{y_k\}_{k\ge 1-n}$ of Eq. (9) with initial conditions such that $(y_0, \dots, y_{1-n}) \in \mathbb{R}^n_+ \setminus \{0\}$.

For both Eqs. (8) and (9), we say that a non-zero equilibrium is a *global stable attractor* if it is a global attractor and it is stable.

Whilst we are mainly interested in studying the case in which A and b are of the form (4), in this section we deal with system