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Attenuant cycles of population models with periodic carrying capacity

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This paper is dedicated to Professor Jim Cushing on the occasion of his 62nd birthday

This paper considers attenuation of cycles generated by periodic difference equations for population dynamics. This study concerns the second conjecture of Cushing and Henson [A periodically forced Beverton-Holt equation, *Journal of Difference Equations and Applications*, **8**, 2002, pp. 1119–1120], which was recently resolved affirmatively by Elaydi and Sacker [Global stability of periodic orbits of nonautonomous difference equations in population biology and the Cushing-Henson conjectures, *Proceedings of the 8th International Conference on Difference Equations and Applications*, Brno, Czech Republic (in press)]. We extend their result and obtain a sufficient condition for attenuation of cycles in population models. This sufficient condition is applicable to a wide class of periodic difference equations with arbitrary period. For an illustration, the result is applied to the Beverton-Holt equation and other specific population models.

Keywords: Periodic difference equations; Average population densities; Beverton-Holt equation; Ricker equation; Global asymptotic stability

AMS Classification Codes: 39A11; 92D25

1. Introduction

In this paper, we consider the following non-autonomous difference equation:

$$\begin{aligned} x_{n+1} &= g\left(\frac{x_n}{K_n}\right)x_n, \\ x_0 &\in \mathbb{R}_+ := [0, +\infty), \\ n &\in \mathbb{Z}_+ := \{0, 1, 2, \ldots\}, \end{aligned} \tag{1}$$

where $g : \mathbb{R}_+ \to \mathbb{R}_+$ is a continuous function which satisfies

$$\begin{aligned} &g(1) = 1 \\ &g(x) > 1 \quad \text{for all} \;\; x \in (0, 1) \\ &g(x) < 1 \quad \text{for all} \;\; x \in (1, \infty), \end{aligned}$$

and $\{K_n\}$ is a periodic sequence such that $K_n > 0$ for all $n \in \mathbb{Z}_+$ and $K_{n+k} = K_n$ for all $n \in \mathbb{Z}_+$ (not necessarily $K_{n+i} \neq K_n$ for all $i, 0 < i < k$). This is a difference equation that

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appears as application in population dynamics. The variable x_n represents a population density at time n and the time dependent parameter K_n is a carrying capacity at time n. Therefore, equation (1) is a population model only with K_n as a periodically fluctuating parameter. By the assumptions of the function g, we see that K_n is a unique positive fixed point of the map $f_n(x) := g(x/K_n)x$.

The following (non-autonomous) Beverton-Holt equation is an example of equation (1):

$$x_{n+1} = \frac{\lambda x_n}{1 + (\lambda - 1)(x_n/K_n)}, \quad \lambda > 1, \ \ K_n > 0, \tag{2}$$

where K_n fluctuates with a period k. It is well known that if K_n is constant (i.e. $K_1 = \cdots = K_k = K_c$), then the positive fixed point K_c of this equation is globally asymptotically stable (i.e. K_c is stable and every solution $\{x_n\}$ with $x_0 > 0$ satisfies $\lim_{n\to\infty}|x_n - K_c| = 0$). It is also known that if K_n fluctuates periodically, then equation (2) can have a periodic solution. By the recent study of Elaydi and Sacker [4], it was shown that for every $k \geq 1$ equation (2) has a unique periodic solution which is globally asymptotically stable (see the next section, and also Cushing and Henson [2] for the case $k = 2$). This result was conjectured by Cushing and Henson [3].

The globally asymptotically stable periodic solution of equation (2) has an ecologically interesting property. Cushing and Henson [2] studied this property, and showed that if $k = 2$ and $K_1 \neq K_2$, then the periodic solution $\{p_1, p_2\}$ of equation (2) satisfies the following inequality:

$$\frac{p_1 + p_2}{2} < \frac{K_1 + K_2}{2}.$$

Since the periodic solution $\{p_1, p_2\}$ is globally asymptotically stable, this inequality implies that the time average of the population density is eventually less than that of the carrying capacity, i.e.

$$\lim_{n\to\infty} \frac{1}{n} \sum_{i=0}^{n-1} x_i < \frac{K_1 + K_2}{2}.$$

This result is of ecological interest because it implies that the environmental fluctuation is deleterious to a population in the sense that its time average of the population density in a fluctuating environment is less than that in a constant environment with the same average. An interesting problem, which is proposed by Cushing and Henson [3], is to investigate whether the Beverton-Holt equation (2) still has this property even if $k \geq 3$. This problem was resolved affirmatively by the recent work of Elaydi and Sacker [5]. The purpose of this paper is to extend their result by analyzing equation (1) which includes the Beverton-Holt equation (2) as a special case.

This paper is organized as follows. In section 2, we introduce the result of global asymptotic stability given by Elaydi and Sacker [4]. In section 3, we investigate the relationship between the time averages of a periodic solution and a carrying capacity of equation (1). In section 4, we apply the results obtained in sections 2 and 3 to the Beverton-Holt equation (2) and other specific population models. The final section includes discussion.

2. Global asymptotic stability

Let $\{x_n\}$ be a solution of equation (1). $\{x_n\}$ is said to be *positive* if $x_n > 0$ for all $n \in \mathbb{Z}_+$. $\{x_n\}$ is said to be *periodic with a period m* (or an *m-cycle*) if $x_{n+m} = x_n$ for all $n \in \mathbb{Z}_+$ (not necessarily $x_{n+i} \neq x_n$ for all i, $0 < i < m$). An m-cycle $\{p_n\}$ is said to be *globally* *asymptotically stable* if it is stable and for every solution $\{x_n\}$ of equation (1) with $x_0 > 0$, there exists an integer l, "asymptotic phase", $0 \le l < k$ such that $\lim_{n\to\infty}|x_n - p_{n+l}| = 0$.

Elaydi and Sacker [4] investigated global asymptotic stability of the following k-periodic difference equation, which includes equation (1) as a special case:

$$x_{n+1} = f_n(x_n), \quad x_0 \in \mathbb{R}_+, \tag{3}$$

where the function $f_n(x)$ is periodic with a period k, i.e. $f_{n+k}(x) = f_n(x)$ for all $n \in \mathbb{Z}_+$ and $x \in \mathbb{R}_+$. By introducing the class $\mathcal{K}$ of a function, Elaydi and Sacker [4] obtained a result of global asymptotic stability of equation (3) as follows:

DEFINITION 1 *A function h belongs to the class* $\mathcal{K}$ *if the following conditions hold:*

- $h : \mathbb{R}_+ \to \mathbb{R}_+$ *is continuous,*
- *h is increasing and concave,*
- *There exist a and b such that* $h(a) > a$ *and* $h(b) < b$.

THEOREM 2 (Elaydi and Sacker [4]). *If* $f_n \in \mathcal{K}$ *for all* $n \in \mathbb{Z}_+$, *then equation (3) has a positive cycle* $\{p_n\}$ *which is globally asymptotically stable.*

Since the Beverton-Holt equation (2) satisfies the assumptions of this theorem, it has a positive cycle which is globally asymptotically stable (Elaydi and Sacker [4]).

3. Attenuant cycles

In this section, we consider the relationship between the time averages of a cycle $\{p_n\}$ and the carrying capacities $\{K_n\}$ of the non-autonomous difference equation (1). An m-cycle $\{p_n\}$ of equation (1) is said to be *attenuant* if $\overline{p} < \overline{K}$, where $\overline{p} = (p_1 + p_2 + \cdots + p_m)/m$ and $\overline{K} = (K_1 + K_2 + \cdots + K_k)/k$. The theorem which gives a sufficient condition for attenuation of cycles of equation (1) is obtained below (Theorem 5). Before giving the main theorem, we obtain some lemmas which are used to prove the main theorem.

LEMMA 3 *If* $g(z)z$ *is concave on some interval (a, b),* $0 < a < b$, *then* $f(x, y) := g(x/y)x$ *is concave on the convex set* $\{(x, y) \in \mathbb{R}^2_+ : ay < x < by\}$.

Proof Since $g(z)z$ is concave, we have

$$g(sz_1 + (1-s)z_2)\ (sz_1 + (1-s)z_2) \ge sg(z_1)z_1 + (1-s)g(z_2)\ z_2$$

for every $s \in (0, 1)$ and $z_1, z_2 \in (a, b)$. Then, for every $s \in (0, 1)$ and $(x_1, y_1), (x_2, y_2) \in \{(x, y) \in \mathbb{R}^2_+ : ay < x < by\}$, we have

$$\begin{aligned} &g\left(\frac{sx_1 + (1-s)x_2}{sy_1 + (1-s)y_2}\right)(sx_1 + (1-s)x_2) \\ &\quad = g\left(t\frac{x_1}{y_1} + (1-t)\frac{x_2}{y_2}\right)\left(t\frac{x_1}{y_1} + (1-t)\frac{x_2}{y_2}\right)(sy_1 + (1-s)y_2) \\ &\quad \ge \left\{tg\left(\frac{x_1}{y_1}\right)\frac{x_1}{y_1} + (1-t)g\left(\frac{x_2}{y_2}\right)\frac{x_2}{y_2}\right\}(sy_1 + (1-s)y_2) \\ &\quad = sg\left(\frac{x_1}{y_1}\right)x_1 + (1-s)g\left(\frac{x_2}{y_2}\right)x_2, \end{aligned}$$

where

$$t = \frac{sy_1}{sy_1 + (1-s)y_2}.$$

Note that x_1/y_1 and x_2/y_2 may be identical. This inequality implies that $f(x,y) = g(x/y)x$ is concave. □

Remark We notice that if $g(z)z$ is concave on some interval (a, b), $0 < a < b$, then $f_n(x) = g(x/K_n)x$ is concave on (aK_n, bK_n).

LEMMA 4 *Let $\{p_n\}$ be a positive m-cycle of equation (1). Suppose that $K_s \neq K_{s+1}$ for some $s \in \{1, 2, \ldots, k\}$. Then $p_i/K_i \neq p_j/K_j$ for some $i, j \in \{1, 2, \ldots, mk\}$.*

Proof Suppose that

$$\frac{p_1}{K_1} = \frac{p_2}{K_2} = \cdots = \frac{p_{mk}}{K_{mk}}. \tag{4}$$

Then we have

$$g\left(\frac{p_1}{K_1}\right) = g\left(\frac{p_2}{K_2}\right) = \cdots = g\left(\frac{p_{mk}}{K_{mk}}\right).$$

By equation (1), this implies

$$\frac{p_2}{p_1} = \frac{p_3}{p_2} = \cdots = \frac{p_1}{p_{mk}}. \tag{5}$$

Since we have $K_s \neq K_{s+1}$, equation (4) implies $p_s \neq p_{s+1}$. Therefore, equation (5) implies that either $p_1 < p_2 < \cdots < p_{mk} < p_1$ or $p_1 > p_2 > \cdots > p_{mk} > p_1$ holds. This is a contradiction. □

THEOREM 5 *Let $\{p_n\}$ be a positive m-cycle of equation (1). Suppose that $K_s \neq K_{s+1}$ for some $s \in \{1, 2, \ldots, k\}$. Assume that $g(z)z$ is strictly concave on an interval (a,b), $0 < a < b$ containing all points $p_i/K_i \in (a, b)$, $i \in \{1, 2, \ldots, mk\}$. Then the cycle $\{p_n\}$ is attenuant.*

Proof By Lemma 4, there exist $i, j \in \{1, 2, \ldots, mk\}$ such that $p_i/K_i \neq p_j/K_j$. Then, by the same argument in the proof of Lemma 3, we see that the strict concavity of $g(z)z$ implies the following strict inequality:

$$g\left(\frac{(p_i/2) + (p_j/2)}{(K_i/2) + (K_j/2)}\right)\left(\frac{p_i}{2} + \frac{p_j}{2}\right) > \frac{1}{2} g\left(\frac{p_i}{K_i}\right) p_i + \frac{1}{2} g\left(\frac{p_j}{K_j}\right) p_j.$$

Hence,

$$\frac{1}{2} f(p_i, K_i) + \frac{1}{2} f(p_j, K_j) < f\left(\frac{1}{2}(p_i + p_j), \frac{1}{2}(K_i + K_j)\right). \tag{6}$$

By Lemma 3, we see that $f(x,y) = g(x/y)x$ is concave on $\{(x,y) \in \mathbb{R}^2_+ : ay < x < by\}$. Since $\{p_n\}$ is a solution of System (1), the following equation holds for all $n \in \mathbb{Z}_+$:

$$p_{n+1} = f(p_n, K_n).$$

Hence, by the concavity of $f(x, y)$ and equation (6), we have

$$\begin{aligned}
\frac{1}{mk}\sum_{n=1}^{mk} p_{n+1} &= \frac{1}{mk}\sum_{n=1}^{mk} f(p_n, K_n) \\
&= \frac{1}{mk}\left\{\sum_{\substack{n=1\\ n\neq i,j}}^{mk} f(p_n, K_n) + 2\left(\frac{1}{2}f(p_i, K_i) + \frac{1}{2}f(p_j, K_j)\right)\right\} \\
&< \frac{1}{mk}\left\{\sum_{\substack{n=1\\ n\neq i,j}}^{mk} f(p_n, K_n) + 2f\left(\frac{1}{2}(p_i + p_j), \frac{1}{2}(K_i + K_j)\right)\right\} \\
&\leq f\left(\frac{1}{mk}\sum_{n=1}^{mk} p_n, \frac{1}{mk}\sum_{n=1}^{mk} K_n\right).
\end{aligned}$$

Furthermore, since $\{p_n\}$ and $\{K_n\}$ are periodic with periods m and k, respectively, we have

$$\overline{p} < f(\overline{p}, \overline{K}),$$

where

$$\overline{p} = \frac{1}{m}\sum_{n=1}^{m} p_n, \quad \overline{K} = \frac{1}{k}\sum_{n=1}^{k} K_n.$$

Since $f(x, \overline{K}) = g(x/\overline{K})x$, the assumptions of g implies that $f(x, \overline{K}) > x$ for all $x \in (0, \overline{K})$ and $f(x, \overline{K}) < x$ for all $x \in (\overline{K}, \infty)$. Hence, we have $\overline{p} < \overline{K}$. □

4. Specific examples

In this section, we apply the results in the previous sections to two types of specific population models.

4.1 Monotone models

Let us consider examples of equation (2) with the assumption that each $f_n(x) = g(x/K_n)x_n$ is monotone. The Beverton-Holt equation (2) and the following equation are of this type:

$$x_{n+1} = \left(\frac{x_n}{K_n}\right)^{a-1} x_n, \quad 0 < a < 1, \tag{7}$$

where $\{K_n\}$ is periodic with a period k and $K_s \neq K_{s+1}$ for some $s \in \mathbb{Z}_+$. By Theorem 2, both equations (2) and (7) have a positive cycle $\{p_n\}$ which is globally asymptotically stable, since the functions $f_{1,n}(x) = g_1(x/K_n)x$ and $f_{2,n}(x) = g_2(x/K_n)x$ are functions of the class $\mathcal{K}$ for all $n \in \mathbb{Z}_+$. By Theorem 5, we see that for every $k \geq 2$ the cycle is attenuant. In fact, defining $g_1(z) = \lambda/(1 + (\lambda - 1)z)$ and $g_2(z) = z^{a-1}$, we have

$$\frac{\mathrm{d}^2}{\mathrm{d}z^2}(g_1(z)z) = -\frac{2(\lambda - 1)\lambda}{(1 + (\lambda - 1)z)^3} < 0$$

and

$$\frac{\mathrm{d}^2}{\mathrm{d}z^2}(g_2(z)z) = (a-1)\,az^{a-2} < 0.$$

These inequalities imply that both $g_1(z)z$ and $g_2(z)z$ are strictly concave on $(0, +\infty)$. Therefore, for every $x_0 > 0$ we have

$$\lim_{n\to\infty}\frac{1}{n}\sum_{i=0}^{n-1}x_i = \frac{1}{m}\sum_{i=0}^{m-1}p_i < \frac{1}{k}\sum_{i=0}^{k-1}K_i. \tag{8}$$

4.2 Non-monotone models

Consider the following (non-autonomous) Ricker equation:

$$x_{n+1} = \exp\left(r\left(1-\frac{x_n}{K_n}\right)\right)x_n, \quad r > 0, \tag{9}$$

where $\{K_n\}$ is periodic with a period k and $K_s \neq K_{s+1}$ for some $s \in \mathbb{Z}_+$. The feature of this equation is different from the other two equations above in the sense that the equation is not monotone, i.e. $f_{3,n} = \exp(r(1-(x/K_n)))x$ is not monotone for every $n \in \mathbb{Z}_+$. Hence, we cannot apply Theorem 2 to this equation to obtain a sufficient condition for global asymptotical stability of cycles. However, by using the result of Zhou and Zou [10], we see that if the following inequality holds:

$$\frac{K_M}{K_m}\exp(r-1) \leq 2, \tag{10}$$

where $K_M = \max_{n\in\{1,2,\ldots,k\}}\{K_n\}$ and $K_m = \min_{n\in\{1,2,\ldots,k\}}\{K_n\}$, then equation (9) has a positive cycle $\{p_n\}$ which is globally attractive, i.e. for every solution $\{x_n\}$ with $x_0 > 0$, there exists an integer $l, 0 \leq l < k$ such that $\lim_{n\to\infty}|x_n - p_{n+l}| = 0$. Under the condition (10), we shall show that the cycle $\{p_n\}$ is attenuant. Defining $g_3(z) = \exp(r(1-z))$, we have

$$\frac{\mathrm{d}^2}{\mathrm{d}z^2}(g_3(z)z) = r\,(rz-2)\exp\,(r(1-z)).$$

Hence, $g_3(z)z$ is strictly concave on $(0, 2/r)$. By equation (9), we see that each $f_{3,n}(x) = \exp(r(1-(x/K_n))x$ $(n = 1, \ldots, k)$ has a maximum at $x = K_n/r$, and $f_{3,n}(K_n/r) = \exp(r-1)$ K_n/r. Hence, the cycle $\{p_n\}$ satisfies

$$p_n \leq \exp(r-1)\frac{K_M}{r}$$

for all $n \geq 0$. Therefore,

$$\max_{i\in\{1,2,\ldots,mk\}}\left\{\frac{p_i}{K_i}\right\} \leq \frac{\exp(r-1)K_M}{rK_m}.$$

By this inequality, we see that if equation (10) holds, then the positive cycle $\{p_n\}$ satisfies $p_n/K_n \in (0, 2/r)$ for all $n \in \mathbb{Z}_+$. This implies that if equation (10) holds, then the interval $(0, 2/r)$ containing all points p_i/K_i, $i = 1, \ldots, mk$, and the cycle $\{p_n\}$ is attenuant. Hence, we see that equation (8) holds for every $x_0 > 0$.

5. Discussion

In this paper, we investigated attenuation of periodic solutions of equation (1), and obtained its sufficient condition (see Theorem 5). This sufficient condition was applied to some specific population models. In particular, this application reconfirmed that a periodic solution of the Beverton-Holt equation (2) is always attenuant as long as the carrying capacity is strictly periodic (i.e. $K_s \neq K_{s+1}$ for some $s \in \mathbb{Z}_+$) (see [5] for a different technique to show this result). Furthermore, it was shown that the result of this paper is applicable not only to the Beverton-Holt equation (2) but also to the other population models. Therefore, our result extends the result of Elaydi and Sacker [5].

We can find some studies on attenuation of periodic solution generated by one dimensional difference equations such as equation (1) (see [2,6]). For example, Cushing and Henson [2] gave a sufficient condition for attenuation under the assumption that each $f_n(x) = g(x/K_n)x, \ (i = 1, \ldots, k)$ is increasing. However, Theorem 5 implies that the monotonicity of f_n is not necessary for the attenuation as long as it is concave on some relevant interval. By using the Ricker equation (9), this point was illustrated. One dimensional difference equations for population dynamics are usually characterized by two parameters: the carrying capacity and the intrinsic growth rate. Equation (1) assumes that the intrinsic growth rate does not fluctuate in time. It is a future work to investigate attenuation of cycles of such equations (see [1] and [6] for the results of attenuation of cycles with small amplitude generated by a general class of differential equations and difference equations, respectively).

It is well known that if f_n is not increasing, equation (1) can have periodic solution even if K_n is constant. This means that the fluctuation of population densities can arise from internal biological factors of a population. For example, the Ricker equation (9) with constant K_n ($K_1 = \cdots = K_k = K_c$) has periodic solutions if $r > 2$ (e.g. see May and Oster [9]). All of these periodic solutions $\{p_n\}$ satisfy $\overline{p} = K_c$ (see [7]). Therefore, in this sense they are not attenuant. An interesting problem is to consider the relationship between the time averages of fluctuating population densities determined by environmental and biological factors (e.g. see [8] for example of attenuant cycles generated by autonomous difference equations).

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