On a Discrete Model of Population Dynamics with Impulsive Harvesting or Recruitment

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Abstract

We consider the difference equation of population dynamics $x_{n+1} = \dfrac{r_n x_n^2}{x_n^2 + A_n}$ which incorporates impulsive perturbations $x_{pk}^+ = b_k x_{pk} - d_k, \quad k = 1, 2, \dots,$ of a harvesting or a recruitment type. The existence of positive solutions, positive periodic solutions and asymptotics are studied.

1 Introduction

The Beverton-Holt difference equation

$$x_{n+1} = \frac{r x_n}{x_n + A} \tag{1}$$

and the equation with

$$x_{n+1} = \frac{r x_n^2}{x_n^2 + A} \tag{2}$$

describe populations that die out completely at each generation and have birth rates that saturate for large population sizes. A comprehensive analysis of (2) can be found, for example, in [1]. This model describes a situation when the species survives if the initial size of the population is greater than a certain threshold. For additional discrete models of population dynamics see [1, 2].

Let us assume that a population with a natural growth described by equation (2) is affected by some harvesting (e.g., fishing or hunting) or recruitment. Let us assume that at every p-th step the system is subject to a perturbation which incorporates the proportional decrease or increase (only bx_{pk} is left at pk-th step, where $b > 0$ and x_{pk} is the value before

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the perturbation) and a deduction d (recruitment $-d$) which does not depend on the size of the population x_{pk}. After the perturbation at step pk the size of the population x_{pk}^{+} becomes

$$x_{pk}^{+} = bx_{pk} - d, \quad k = 1, 2, \dots\ , \tag{3}$$

where x_{pk} is the size of the population at step pk before the impulsive perturbation.

The impulsive conditions include both cases of the proportional and constant harvesting or recruitment. First let us consider the harvesting case. A proportional part can be interpreted as fishery or hunting with a constant fishing (hunting) effort, while a constant part can correspond to hunting with a constant number of licenses or predation with a constant number of predators that control a certain territory. Alternatively, if the model describes a farm with finite resources, the proportional reduction can correspond to some kind of taxation, while the constant part can describe a producer's consumption. In both examples the problem of non-extinction of the population becomes a description of a reasonable hunting rate or of a judicious taxation. Next, suppose we have impulsive conditions of mixed harvesting/recruitment type. For example, if $0 < b < 1$, $d < 0$, then the constant recruitment together with the natural population growth should compensate hunting or predation with a constant effort (a constant number of predators). If $b > 1$, $d > 0$, then a constant deduction should be compensated by the natural growth and the proportional recruitment. From the mathematical point of view the proportional harvesting can be included in the growth rate r while the constant deduction term d can lead to new effects in the behavior of the system.

2 A model with constant coefficients

Everywhere in the model we assume $A > 0$, $r > 0$, $b > 0$. For simplicity let us first consider $p = 1$ in (3) (later we will discuss the general case as well). Then

$$x_{n+1} = b\left(\frac{rx_n^2}{x^2 + A}\right) - d = \frac{brx_n^2}{x_n^2 + A} - d = \frac{(br - d)x_n^2 - Ad}{x_n^2 + A}.$$

Thus we study the equation

$$x_{n+1} = \frac{\beta x_n^2 - Ad}{x_n^2 + A}, \quad \beta = br - d. \tag{4}$$

This model leads to the following cases: $d > 0$ (then it should be $\beta > 0$ to avoid the immediate extinction of the population), $d < 0$ (then $\beta = br - d > 0$ since $b > 0$). It is also to be noted that for any sign of d we have $\beta + d = br > 0$.

Case 1: $d > 0$. Denote

$$g(x) = x^3 - \beta x^2 + Ax + Ad, \tag{5}$$

$$\underline{x} = \frac{\beta - \sqrt{\beta^2 - 3A}}{3}, \ \bar{x} = \frac{\beta + \sqrt{\beta^2 - 3A}}{3}. \tag{6}$$

Lemma 1 *Let $\beta > 0, d > 0$.*
1) If $\beta^2 > 3A$ and $g(\bar{x}) < 0$ then $g(x) = 0$, where $g(x)$ is defined in (5), has exactly 2

positive solutions x^- *and* x^+*, then for any initial value* x_0 *satisfying* $x_0 > x^-$ *the solution of (4) is positive and tends to* x^+*. If* $\beta^2 \geq 3A$ *and* $g(\bar{x}) = 0$*, then* $x^- = x^+ > 0$*. In this case any solution of (4) with* $x_0 \geq x^+$ *is positive and tends to* x^+*, any solution with* $x_0 < x^+$ *is eventually negative.*
2) If either $\beta^2 < 3A$ *or* $\beta^2 \geq 3A$ *together with* $g(\bar{x}) > 0$*, then all solutions of (4) are eventually negative.*

Proof. First let us mention that since $d > 0$, $\beta > 0$, then the reproduction function is increasing for $x > 0$:

$$f(x) = \frac{\beta x^2 - Ad}{x^2 + A} = \beta - \frac{A(\beta + d)}{x^2 + A}, f'(x) = \frac{2A(\beta + d)x}{(x^2 + A)^2} > 0, \ x > 0,$$

and the reproduction curve

$$y = f(x) = \frac{\beta x^2 - Ad}{x^2 + A} \tag{7}$$

can intersect $y = x$ three times or only once (we get a cubic equation) for $x > 0$, there is also a case of two distinct roots, one of which is multiple, or one triple root. Here

$$\lim_{x \to \pm\infty} \frac{\beta x^2 - Ad}{x^2 + A} = \beta > 0$$

and we assumed $d > 0$, so $f(0) = -d < 0$ and one point of intersection is in the domain $x < 0$. The equation $x = f(x)$ has a positive solution if and only if the cubic equation $g(x) = 0$, where $g(x)$ is defined in (5), has a positive solution. Since $g(0) > 0$ this means that $g(x^*) < 0$ for some $x^* > 0$. The derivative is $g'(x) = 3x^2 - 2\beta x + A$ and $\beta > 0$; if $\beta^2 > 3A$, then $g(x)$ has
a local maximum at $\underline{x} = \dfrac{\beta - \sqrt{\beta^2 - 3A}}{3}$ and a local minimum at $\bar{x} = \dfrac{\beta - \sqrt{\beta^2 - 3A}}{3}$.
Consequently, if $g(\bar{x}) < 0$, then the equation (5) has two positive solutions x^- and x^+, where x^+ is a global attractor for any $x_0 > x^-$. If $x_0 < x^-$, then the solution is eventually negative.

In the case $g(\bar{x}) = 0$ we have a multiple root $x^- = x^+$, all solutions with $x_0 \geq x^+$ are positive and tend to x^+, while all solutions with $x_0 < x^+$ are eventually negative.

Finally, if $\beta^2 < 3A$, then g is increasing and so $g(x) > 0$ for any $x > 0$. This means that all solutions of (4) are eventually negative.

For additional illustration see Fig. 1.

Remark. It is to be noted that in this case any positive solution is monotone: it is increasing if x_0 is less than an attractor x^+ and is decreasing if $x_0 > x^+$. To some extent this complies the logistic growth model: if the size of the population is less than the saturation level, then the solution tends to this level from below; otherwise it tends from above. The behavior of solutions of (4) has the following feature of (2): the species extincts if the initial level is less than a certain positive quantity (which is the least positive equilibrium point x^- if it exists, or infinity, if there no real positive equilibrium points).

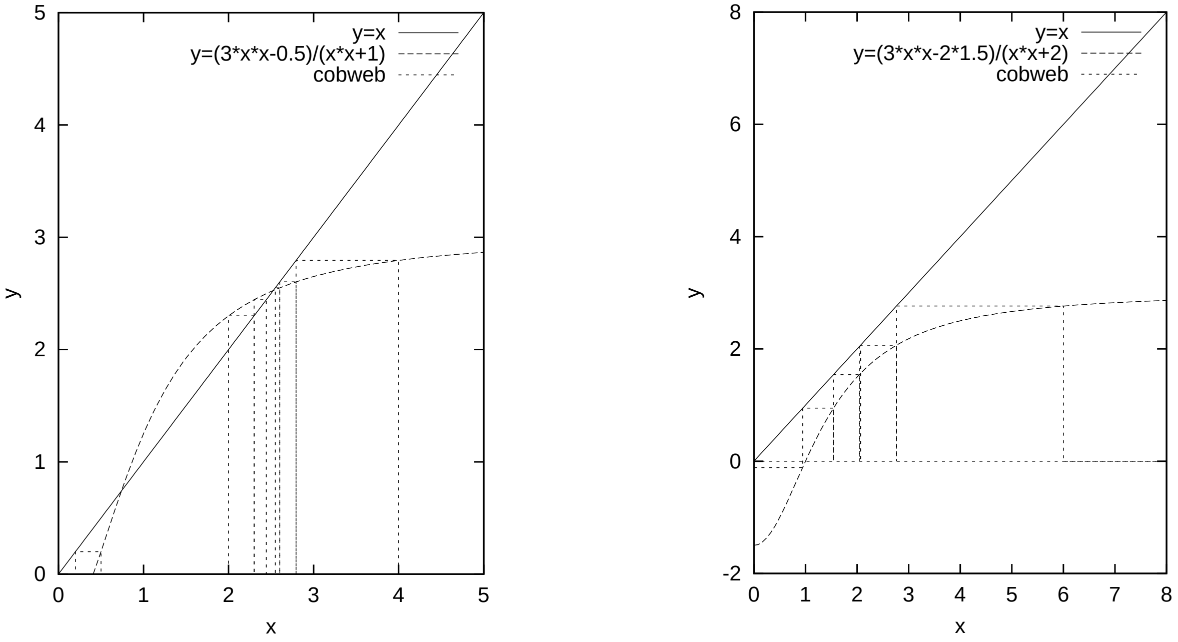

Figure 1: $y = f(x) = (\beta x^2 - Ad)/(x^2 + A)$ and $y = x$ in the following cases: a) $\beta = 3, A = 1, d = 0.5$, with two positive equilibrium points, the first point is a repeller and the second one is an attractor; b) $\beta = 3, A = 2, d = 1.5$, with no positive equilibrium points; all solutions extinct

Case 2: $d < 0$.

Lemma 2 *Let* $\beta > 0, d < 0$.
1) Suppose the cubic equation $g(x) = 0$*, where* g *is defined by (5), has 3 positive solutions, probably multiple (this is satisfied if and only if* $g(\underline{x}) \geq 0$ *and* $g(\bar{x}) \leq 0$*, where* $\underline{x}, \bar{x}$ *are defined in (6)), these solutions will be denoted by* x^-, x^0 *and* x^+*. If* x^-, x^0, x^+ *are distinct, then* x^- *is an attractor for the initial conditions* $0 \leq x_0 < x^0$*,* x^+ *is an attractor for any* $x_0 > x^0$*, the equilibrium point* x^0 *is a repeller. If* $x^- = x^0$ *(*$g(\underline{x}) = 0$*), then* x^- *is an attractor for* $0 \leq x_0 \leq x^-$ *and* x^+ *is an attractor for* $x_0 > x^-$*. If* $x^0 = x^+$ *(* $g(\bar{x}) = 0$*) then* x^- *is an attractor for* $0 \leq x_0 < x^0$*,* $x^0 = x^+$ *is an attractor for any* $x_0 > x^0$*. If* $x^- = x^0 = x^+$ *then we have a global attractor (for all* $x_0 \geq 0$*). All solutions of (4) are monotone.*
2) Suppose the equation $g(x) = 0$ *has only one real solution* x^- *which is positive. Then* x^- *is a global attractor for any initial condition* x_0 *and all solutions of (4) are monotone.*

Proof. Let us note that since $\beta + d > 0$ then $f(x)$ is increasing for $x > 0$

$$f(x) = \frac{\beta x^2 - Ad}{x^2 + A} = \beta - \frac{(\beta + d)A}{x^2 + A}.$$

The equations $x = f(x)$ and $g(x) = 0$ have the same number of roots, where g is defined in (5). Since $g(0) = Ad < 0$, then g has either three positive roots or only one positive root. If as in 1) we assume there are three positive solutions x^-, x^0 and x^+, then $f(x)$ is increasing, $f(x) > x$ for $0 < x < x^-$ and $f(x) < x$ for $x^- < x < x^0$, $f(x) > x$, $x^0 < x < x^+$, $f(x) < x$,

$x > x^+$. Thus we have two attractors x^- and x^+, the first for $x_0 < x^0$ and the second for $x_0 > x^0$. The equilibrium point x^0 is a repeller. The cases when some of the roots coincide are treated similarly.

Let as in 2) be only one positive root x^-; since $\beta + d > 0$ then $f(x)$ is also increasing, $f(x) > x$, $x < x^-$, and $f(x) < x$, $x > x^-$. Here x^- is a global attractor for any $x_0 > 0$, and all solutions are monotone.

For additional illustration see Fig. 2.

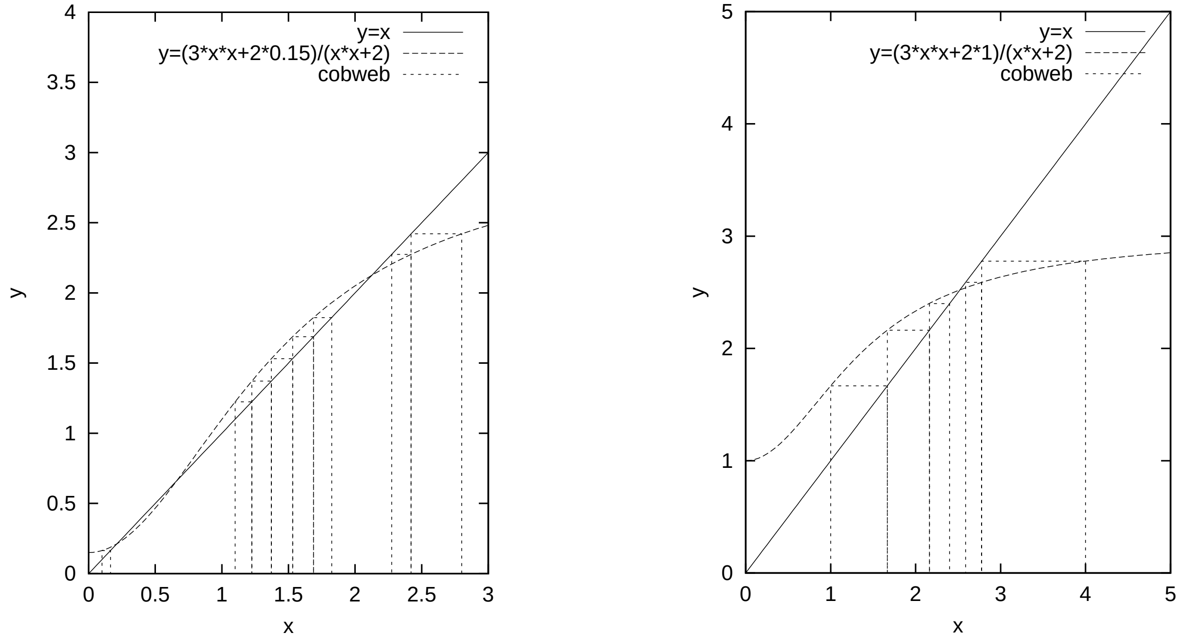

Figure 2: $y = f(x) = (\beta x^2 - Ad)/(x^2 + A)$ and $y = x$ in the following cases: a) $\beta = 3, A = 2, d = -0.15$, with three positive equilibrium points, the first and the third points are attractors and the second point is a repeller; b) $\beta = 3, A = 2, d = -1$, with one positive equilibrium, which is a global attractor

Remark. If we could consider $\beta + d < 0$, then all solutions of (4), with $x_0 > 0$, would be positive and oscillating about x^-. Really, if $\beta + d < 0$ then $f'(x) < 0$, when $x > 0$, $f(x)$ is decreasing and $\beta < f(x) < x^-$, if $x > x^-$, $f(x) > x^-$, if $0 < x < x^-$. Thus all solutions are positive and the sequence $\{x_n - x^-\}$ is alternating.

3 A model with variable coefficients

Now let us consider the difference equation (4) with nonconstant coefficients

$$x_{n+1} = \frac{\beta_n x_n^2 - A_n d_n}{x_n^2 + A_n}, \quad \beta_n = b_n r_n - d_n, \tag{8}$$

which describes the model with a non-constant rate of growth

$$x_{n+1} = \frac{r_n x_n^2}{x_n^2 + A_n} \tag{9}$$

which is subject to impulsive perturbations of type (3), with nonconstant b_k, d_k and $p = 1$:

$$x_n^+ = b_n x_n - d_n. \tag{10}$$

Then we get a cubic equation with nonconstant coefficients

$$x^3 - \beta_n x^2 + A_n x + A_n d_n = 0. \tag{11}$$

Theorem 1 *Suppose $\beta_n > 0$, $d_n > 0$. Let x_n^- be the smallest and x_n^+ be the greatest positive solutions of (11), respectively (if they exist).*
1) If $x_0 < \inf_n x_n^-$ (here only existing x_n^- are included in the right hand side) then any solution of (8) extincts (either becomes eventually negative or tends to zero);
2) If (11) has a positive solution for any n, $\sup_n x_n^- < \inf_n x_n^+$ and $x_0 > \sup_n x_n^-$, then the solution of (8) is positive and for any ε it eventually belongs to the neighbourhood $(\inf_n x_n^+ - \varepsilon, \sup_n x_n^+ + \varepsilon)$.

Proof. 1) If $x_0 < \inf_n x_n^-$ then $x_1 < x_0 < \inf_n x_n^-$. Suppose the sequence $\{x_n\}$ is positive. Then it is decreasing (see Lemma 1: for every n it has a positive repeller and a negative attractor). Thus this sequence has a nonpositive limit which means that the sequence either becomes negative or tends to zero. The latter case means that the negative attractors also tend to zero.
2) If $x_0 > \sup_n x_n^- > 0$ then so is any $x_n > \sup_n x_n^- > 0$. Really, $\sup_n x_n^- < x_n < x_n^+$ implies $x_n^+ > x_{n+1} > x_n > \sup_n x_n^-$ and $x_n > x_n^+$ implies $x_n > x_{n+1} > x_n^+ > \sup_n x_n^-$. Thus for any $x_0 > \sup_n x_n^-$ the solution is positive. Since x_n^+ is an attractor for the n-th equation then (see Lemma 1 and Fig.1) $\left|x_{n+1} - x_n^+\right| < \left|x_n - x_n^+\right|$. Once $x_k < \sup_n x_n^+$ then all the subsequent elements of the sequence $\{x_n\}$ do not exceed $\sup_n x_n^+$. Each of equalities (8) has an attractor x_n^+ not exceeding $\sup_n x_n^+$, so if all $x_k > \sup_n x_n^+$ then the sequence tends to $\sup_n x_n^+$ and for any ε eventually does not exceed $\sup_n x_n^+ + \varepsilon$. Similarly we can show that if all $x_k < \inf_n x_n^+$, then for any ε eventually $x_k > \inf_n x_n^+ - \varepsilon$.

Theorem 2 *Suppose $\beta_n > 0, d_n < 0$. Let x_n^+ be the greatest positive solution of (11). Then any solution of (8) with $x_0 > 0$ is positive and for any ε the solution of (8) eventually does not exceed $\sup_n x_n^+ + \varepsilon$.*

Proof. By Lemma 2 any solution of (8) with $x_k > 0$ satisfies $x_{k+1} > 0$, thus any solution with $x_0 > 0$ is positive. Since the greatest positive solution is an attractor then for any ε the solution eventually does not exceed $\sup_n x_n^+ + \varepsilon$.

Now let us proceed to the case when d_n has no definite sign; there is harvesting at certain steps and recruitment at the other steps.

Theorem 3 *Suppose $\beta_n > 0$. For $d_n > 0$ denote by y_n^- the smallest and by y_n^+ the greatest positive solutions of (11), respectively (if they exist). For $d_n < 0$ denote by z_n^-, z_n^0, z_n^+ successive solutions of (11) (there is always a positive solution, if there is the only solution we assume it is z_n^-).*
If $\inf_n y_n^- \le \inf_n z_n^-$ then any solution of (8) with $x_0 > \sup_n y_n^-$ is positive.

Proof. Suppose $x_n > \sup_n y_n^-$. First let the n-th equation have $d_n > 0$. Then $x_n > y_n^-$ and $x_{n+1} > y_n^- > \inf_n y_n^-$ since y_n^- is a repeller.

Now assume $d_n < 0$. If $x_n > z_n^-$, then $x_{n+1} > z_n^- > \inf_n z_n^- \geq \inf_n y_n^-$ (see Fig.2); if $x_n < z_n^-$, then $x_{n+1} > x_n > z_n^- > \inf_n z_n^- \geq \inf_n y_n^-$. The induction step concludes the proof.

4 Models which are not Perturbed at Each Time Step

Now let us proceed to the case when the impulsive perturbation does not occur at every time step (in (3) $p > 1$). Unlike (1) the expression for x_{n+2} as a function of x_n for (2) has the form different from (2):

$$x_{n+2} = \frac{rx_{n+1}^2}{x_{n+1}^2 + A} = \frac{r\frac{(rx_n^2)^2}{(x_n^2+A)^2}}{\frac{(rx_n^2)^2}{(x_n^2+A)^2} + A} = \frac{r^3x_n^4}{r^2x_n^4 + A(x_n^2 + A)^2}.$$

Similarly,

$$x_{n+p} = \frac{\bar{r}x_n^{2^p}}{T_p(x_n)}, \quad \bar{r} = r^{2^p-1}, \tag{12}$$

where $T_p(x)$ is a polynomial of degree 2^p which involves only even degrees, all coefficients of T_p are positive, $T_p(0) > 0$. One can easily observe that

$$T_1(x) = x^2 + A, \quad T_2(x) = r^2x^4 + A(x^2 + A)^2.$$

The expression which appears in the numerator when we compute x_{n+1}, x_{n+2}, x_{n+3}, $\ldots$, x_{n+p} is rx_n^2, $r^3x_n^4$, $r^7x_n^8$, $\ldots$, $r^{2^p-1}x_n^{2^p}$, respectively. Therefore it can be easily deduced that

$$T_1(x) = x^2 + A, \quad T_{k+1}(x) = (r^{2^k-1}x^{2^k})^2 + A(T_k(x))^2, \tag{13}$$

which defines the sequence of polynomials $T_k(x)$.

Together with the impulsive perturbation (3) we have

$$x_{n+p} = \frac{\bar{r}bx_n^{2^p} - dT_p(x_n)}{T_p(x_n)}. \tag{14}$$

Let us introduce the following cubic equation

$$g(x) = xT_p(x) - \bar{r}bx_n^{2^p} + dT_{2p}(x_n) = 0. \tag{15}$$

In the case $d > 0$ there is an even number of positive (probably coinciding) solutions of (15). If $d < 0$ there exists at least one positive solution of (15). Similar to the case $p = 1$ we get the following results.

Theorem 4 *Suppose $d > 0$ and the equation (15) has a positive real solution. Let x^- be the least positive solution of (15). Then any solution of (2), (3), with $x_0 \geq x^-$, is positive. If (15) has no positive solutions, then all solutions of (2), (3) are eventually negative.*

Proof. The reproduction function for (12)

$$f_1(x) = \frac{\bar{r}x^{2^p}}{T_p(x)}$$

is increasing as a composition of increasing functions $h(x) = \dfrac{rx^2}{x^2 + A}$. For

$$f(x) = \frac{\bar{r}bx^{2^p} - dT_p(x)}{T_p(x)} = bf_1(x) - d$$

we have $f'(x) = f_1'(x) > 0$ since $b > 0$. Thus $f(x)$ is increasing, $f(0) < 0$. The first positive root of (15) x^- is a repeller and $f(x) > x^-$ for any $x > x^-$. Hence $x_n > x^- > 0$ for any $x_0 \geq x^-$ and x_n tends to a negative attractor for any $x_0 < x^-$ and so is eventually negative.

Similarly the following result can be obtained.

Theorem 5 *Suppose $d < 0$. Then all solutions of (2), (3) with $x_0 > 0$, are positive.*

Now let us consider an equation with nonconstant coefficients (9), and nonconstant impulsive perturbations

$$x_{pk}^+ = b_k x_{pk} - d_k, \quad k = 1, 2, \dots\ , \tag{16}$$

$$x_{p(k+1)} = \frac{\bar{r}_k b x_{pk}^{2^p} - d_k T_k(x_{pk})}{T_k(x_{pk})}, \tag{17}$$

where T_k are polynomials of degree 2^p.

Let us also introduce the following cubic equation

$$g_k(x) = xT_k(x) - \bar{r}_k b_k x^{2^p} + d_k T_k(x) = 0. \tag{18}$$

Theorem 6 *Suppose $d_k > 0$ and the equation (18) has a positive real solution for any k. Let x_k^- be the least positive solution of (18). Then any solution of (9), (16), with $x_0 \geq \sup_k x_k^-$, is positive. If $x_0 < \inf_k x_k^-$, then all solutions of (9), (16) are eventually negative.*

Theorem 7 *Suppose $d < 0$. Then all solutions of (9), (16), with $x_0 > 0$, are positive.*

Finally, let us consider the case when r_n and A_n are nonconstant but periodic with the period p and b, d are constant. Nonconstant rates of population growth r_n, A_n can describe seasonal changes while harvesting (recruitment) is at a constant rate once a year. Let us study the existence of positive periodic solutions for (9), (3) in the case of periodic parameters.

Theorem 8 *Let r_n, A_n be positive periodic sequences with period p.*
1) Suppose $d > 0$. Then (9), (3) has a positive periodic solution if and only if (15) has a positive root (in the periodic case the polynomial T_k will be the same for any k).
2) Suppose $d < 0$. Then (9), (3) has a positive periodic solution.

Proof. The dynamics of (9), (3) is completely described by the properties of the equation (14). The reference to Theorems 4,5 completes the proof.

Remark. Theorem 8 claims that if the constant part is of the recruitment type, then, independently of parameters, there exists a positive periodic solution. If we have a constant harvesting, then for certain value of parameters all solutions extinct in a finite time (independently of the initial value); for other values of parameters the solution is positive and asymptotically periodic unless the initial size of the population is less than a critical value.

References

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