On linear perturbations of the Ricker model [☆]

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Abstract

A class of linearly perturbed discrete-time single species scramble competition models, like the Ricker map, is considered. Perturbations can be of both recruitment and harvesting types. Stability (bistability) is considered for models, where parameters of the map do not depend on time. For models with recruitment, the result is in accordance with Levin and May conjecture [S.A. Levin, R.M. May, A note on difference delay equations, Theor. Pop. Biol. 9 (1976) 178]: the local stability of the positive equilibrium implies its global stability. For intrinsic growth rate $r \to \infty$ the way to chaos is broken down to get extinction of population for the depletion case and to establish a stable two-cycle period for models with immigration. The latter behaviour is also studied for models with random discrete constant perturbations of recruitment type. Extinction, persistence and existence of periodic solutions are studied for the perturbed Ricker model with time-dependent parameters.
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1. Introduction

Many non-linear dynamical systems demonstrate chaotic behaviour, for example, the well known Ricker model [21]

$$x_{n+1} = x_n \exp[r(1 - x_n)] \tag{1}$$

or the logistic map

$$x_{n+1} = \max\left\{ rx_n\left(1 - \frac{x_n}{K}\right), 0 \right\} \tag{2}$$

for r large enough (following [23,29], any positive r is allowed for the truncated map). However in ecological systems chaotic dynamics is difficult to observe [3,28]. Perturbations are usually believed the main reason for this. McCallum [17] found that even a constant perturbation

$$x_{n+1} = x_n \exp[r(1 - x_n)] + \lambda \tag{3}$$

can significantly change the properties of (1). It was established [17,26] that with the growth of r the period-doubling route to chaos, which is characteristic to (1), will break down for (3) and will give rise to a stable two-cycle.

The assumption that $\lambda > 0$ is a constant may be restrictive. In [27] the model (3) was considered, where λ was not a constant but a discrete uniform random variable with the distribution $P\{\lambda = a_i\} = p_i$, $i = 1, \ldots, n$, $0 < a_i < 1$. It was proven (Theorem 2.1 in [27]) that for r sufficiently large, there are $n(n + 1)$ blurred orbits in (3). Note that in [17,26,27] only positive perturbations of the Ricker population model were considered (immigration) which is also not always realistic. In many cases perturbations include harvesting of, as well as immigration to populations. The drop of blue pike annual catches from 10 million pounds to less than one thousand pounds in mid-1950s [2], the reduction of Great Britain's grey partridge population in 1952 [1,20] and the collapse of the Peruvial anchovy population in 1973 [6] are examples of this dramatic decrease [23]. One explanation of this phenomenon was multistability of ecological models when small environmental changes can push the system from the positive equilibrium state to the zero equilibrium state [4,13]. Simple continuous models which exhibit this behaviour involve constant rate of harvesting or predation [5]. In 1996 the general class of discrete maps was discussed [11] concerned with so called Allee functions; for these maps extinction is inevitable for too high or too low population densities.

The Ricker model with depletion

$$x_{n+1} = x_n \exp[r(1 - x_n)] - d \tag{4}$$

was considered in [24] and on some general basis of Allee functions with negative Schwarzian derivative in [23]. Like in (3), for large r the chaotic behaviour also cannot be observed in (4); in the latter case due to extinction of the population. For the growth rate $r < r^* \approx 2.6$ the population (4) demonstrates bistability for small d and goes to extinction in a finite number of generations for $d > d(r)$ [23]. If $r > r^*$, then for high depletion rates d the population goes to extinction in a finite number of generations. At a certain value of d the population survives and demonstrates period doubling. If the depletion rate d continues to decrease then the size of the attracting interval increases until it collides with the boundary of the origin's immediate basin of attraction. This collision results in an essential extinction. For large r the domain of population persistence is small ($d_1 < d < d_2$), with d_1, d_2 growing with the growth of r.

We suggest that, in addition to constant immigration or depletion, some proportional coefficient be introduced at each step. Certainly, with an appropriate change of variables, this model can be reduced to the previous one (Eqs. (3) or (4), respectively) as far as the coefficient of $x_n\exp(-x_n)$ exceeds one. However if it is less than one, such reduction is no longer possible. Moreover, if in the model $x_{n+1} = rx_n\exp(-x_n) + u$ both $r < 1$ and $u \leqslant 0$, then extinction is inevitable. Populations which can go to extinction in the absence of immigration are considered, for instance, in [27]. One example is migrating wheat aphids, which is an agricultural pest [8,31]. In some cold winter wheat production regions, the amount of the local overwintering population is low since few aphids can survive in winter. We suggest that this can be modeled by the proportional decrease of the population after the winter season. The major portion of the initial population in spring migrates from spaces where they overwinter (migration term λ in (3)). In summer, depending on the weather, the aphid population may grow with a high reproduction rate. After wheat harvest most aphids migrate (corresponding (4)) and only few of remaining survive the winter. Such dynamics is common in northern winter wheat production regions in China [27].

Another example [27] is annual dynamics of *Puccinia striiformnia*, a fungal pathogen causing stripe rust disease of wheat in central and northern China [32,33]. The fungus can survive and grow all year round in mountainous northwest wheat production regions. However, the fungus cannot survive over summer in the northeastern and central wheat production regions. In these regions, annual epidemics start with airborne spores moved in by air currents from the northwest wheat production regions. Overall, such dynamics is characteristic for some migrating insect and airborne pathogen populations. Such characteristics of this dynamics as important role of migrations early in growing seasons, high reproduction rates and the level of migration independent of the density of the local population allowed it to be matched to (3) in the domain of reproduction rates where chaos is changed to a stable two-cycle.

The connection between perturbations like immigration and the break of chaos was discovered in some other models [22], some population models do not have this property [7]. The connection of chaos and perturbations for discrete models was also considered for random perturbations [9,27].

It is well known that difference equations are closely related to differential equations, delay differential equations and differential equations with piecewise constant arguments (see, for example, [10,12,15,18]). It is also possible to demonstrate that asymptotic properties of impulsive differential equations with piecewise constant arguments can be reduced to discrete maps subject to linear perturbations.

In addition to the Ricker equation, we consider a more general model, such that the reproduction curve has the following properties: it vanishes at $x = 0$, increases for $x < c$, decreases for $x > c$ and tends to zero at infinity. This can be thought of as representing a situation in which scramble competition occurs (limited resources are distributed uniformly) [4]. The following novel elements are proposed for scramble competition ecological models:

1. The possibility of the proportional reduction coefficient which can, for example, model the overwintering survival rate. This sometimes leads to the growth rate which is less than one; in the absence of migration, extinction of the population is inevitable. However with a certain rate of migration, persistence of solutions is observed.

2. Perturbations of both recruitment and harvesting type are considered; moreover, the model involves variable perturbation and reproduction rates. Problems of persistence and attracting sets can be considered in the case of variable parameters.

Let us note that we consider truncated models: the left hand side of the difference equation is assumed to be equal to zero, if the right hand side is negative.

The paper is organized as follows. Section 2 involves some results for the general model with constant coefficients which are applied in Section 3 to the Ricker equation with variable parameters. Existence of periodic solutions is considered in the case of periodic parameters. In Section 4 the following problem is discussed: for which models with constant or discrete random recruitment does a stable two cycle period exist, when the intrinsic growth rate is large enough?

2. A model with constant coefficients

Consider a truncated discrete map with a recruitment (harvesting) constant term v

$$x_{n+1} = \max\{g(x_n) + v, 0\}, \tag{5}$$

where function $g(x)$ satisfies the following conditions:

(A1) g is continuous, $g(x) \geqslant 0$, $g(0) = 0$, $\lim_{x\to\infty} g(x) = 0$;
(A2) there exists $c > 0$, such that $g'(x) > 0$, $x < c$, and $g'(x) < 0$, $x > c$;
(A3) $g''(x) < 0$, if $x < c$.

Note that $g(x)$ has the only positive global maximum point $x = c$. Denote

$$f(x) = g(x) + v. \tag{6}$$

In order to consider truncated functions $g(x)$, which are, generally speaking, not differentiable at the truncation point and do not have a negative derivative after this point, since they are constant, we introduce some generalization of (A2):

(A2*) there exists $c > 0$, such that $g'(x) > 0$, $x < c$, g is non-increasing for $x > c$ and c is a local maximum.

As one of our main models, consider a perturbed Ricker model

$$x_{n+1} = kx_n e^{r(1-x_n)} + u, \tag{7}$$

where $k > 0$, u may be positive or negative. The perturbation is equivalent to harvesting (for $0 < k < 1$) or to recruitment (for $k > 1$) of a proportional part of the population and some constant addition or deduction at each step. Thus $x_{n+1} = (ke^r)x_n e^{-rx_n} + u = \bar{r}x_n e^{-rx_n} + u$, where $\bar{r} = ke^r$. Making the substitution $y_n = rx_n$, we get $\frac{y_{n+1}}{r} = \bar{r}\frac{y_n}{r}e^{-y_n} + u$, or $y_{n+1} = \bar{r}y_n e^{-y_n} + ur$. After denoting $v = ur$ we obtain the difference equation which involves two parameters only:

$$y_{n+1} = \bar{r}y_n e^{-y_n} + v. \tag{8}$$

It is easy to show that a different type of linear perturbation (perturbation at the beginning of the step) leads to the same model. In fact, if in

$$x_{n+1} = (ax_n + b)e^{r(1-x_n)} \tag{9}$$

we make the substitution $z_n = \frac{r}{a}(ax_n + b)$, then $x_n = \frac{1}{r}z_n - \frac{b}{a}$ and (9) is equivalent to

$$z_{n+1} = cz_ne^{-z_n} + d, \tag{10}$$

where $c = a\exp\left\{r\left(1 + \frac{b}{a}\right)\right\}$, $d = \frac{rb}{a}$. We can see that Eqs. (10) and (8) have the same form. Consequently, both forms of the linearly perturbed equation are equivalent. Eq. (8) is also equivalent to the perturbed Ricker model discussed in [27]

$$N_{t+1} = N_t \exp[r(1 - N_t)] + \varepsilon, \tag{11}$$

if t in (11) is an integer and $\bar{r} > 1$, $v > 0$ in (8).

For equations with discrete time our model is more general since we can assume $0 < \bar{r} < 1$ (for $v > 0$ in (8), certainly) and can assume $v < 0$ (for $\bar{r} > 1$). Further we change the $\bar{r}$ notation by r (the meaning of $\bar{r}$ is the growth rate, as r in (11), only $\bar{r} = \ln r$) and study the following perturbed Ricker model

$$x_{n+1} = rx_ne^{-x_n} + v. \tag{12}$$

Example 1. For the perturbed Ricker model (12) the function $g(x) = rxe^{-x}$ satisfies (A1)–(A3). In fact,

$$g(0) = 0 = \lim_{x\to\infty} g(x) \tag{13}$$

gives (A1),

$$g'(x) = r(1 - x)e^{-x} \tag{14}$$

implies (A2) with $c = 1$,

$$g''(x) = r(x - 2)e^{-x}$$

implies (A3). Function $g(x)$ has a maximum at the point $x = 1$ and an inflection point at $x = 2$, where the minimum of the derivative is attained.

Example 2. The truncated logistic map

$$x_{n+1} = \max\left\{\max\left\{rx_n\left(1 - \frac{x_n}{K}\right), 0\right\} + v, 0\right\} \tag{15}$$

has $g(x) = \max\{rx_n(1 - x/K), 0\}$, which satisfies (A1), (A2*) and (A3), with $c = K/2$.

Generally, a function satisfying (A1)–(A3) is not necessarily differentiable at $x = c$, for example, $g(x) = \begin{cases} x\exp r(1 - x), & x < 1 \\ \frac{1}{x}, & x \geqslant 1 \end{cases}$ satisfies (A1)–(A3) but is not differentiable at the maximum point $x = 1$.

We will use the following well known result.

Lemma 1. *Suppose f is a differentiable function and for the solutions of the difference equation* $x_{n+1} = f(x_n)$, *with* $x_0 \in \Omega$, *we have* $x_n \in [a,b]$ *for n large enough. Suppose in addition there is an equilibrium point* $x^* = f(x^*) \in [a,b]$ *and* $|f'(x)| < \lambda < 1$ *for* $x \in (a,b)$. *Then* x^* *is an attractor for any initial condition in the set* Ω.

First consider the existence of equilibrium points of (5).

Theorem 1. Suppose (A1)–(A3) hold. (1) *Let* $v > 0$. *Then Eq.* (5) *has the only positive equilibrium point* N^*. (2) *Let* $v < 0$. *If* $g'(0) < 1$, *then for any* $v < 0$ *all solutions go to extinction. If* $g'(0) > 1$, *then there exists* x^*, *such that* $g'(x^*) = 1$. *In this case for* $v > x^* - g(x^*)$ *there are two positive equilibria, for* $v = x^* - g(x^*)$ *there is one positive equilibrium, for* $v < x^* - g(x^*)$ *all solutions go to extinction.*

Proof. (1) Let us prove that for $v > 0$ a positive equilibrium point exists and is unique. Define $h(x) = x - f(x)$. We have $h(0) = -v < 0$ and $h(x) \to \infty$ as $x \to \infty$. Thus there exists an equilibrium point $h(N^*) = 0$. Further, $h'(x) = 1 - g'(x)$, so by (A2) $h(x)$ is increasing for $x > c$. By (A3) $g'(x)$ is decreasing for $0 < x < c$, so either $g'(0) < 1$ or there exists $\zeta \in (0,c)$, such that $h'(x) < 0$ for $x \in (0,\zeta)$ and $h'(x) > 0$ for $x > \zeta$. In the former case h is monotone increasing, thus the equilibrium point is unique. In the latter case $h(x) \leqslant -v < 0$ for $x \in [0,\zeta)$, since $h(0) = -v$ and $h(x)$ is decreasing for $x \in (0,\zeta)$, thus there is no equilibrium point in $(0,\zeta)$. Function $h(x)$ is monotone for $x > \zeta$, so the equilibrium point is unique.

(2) Now let $v < 0$. Then $h(x) = x - g(x) - v$ has an equilibrium point if and only if $h(x) \leqslant 0$ for some x. If $g'(0) < 1$, then h is increasing for any x, $g(0) = -v > 0$, thus there is no positive equilibrium point, all solutions go to extinction.

If $g'(0) > 1$, then h has a critical point (minimum) $x^*: h'(x^*) = 1 - g'(x^*) = 0$. In the case $h(x^*) = x^* - g(x^*) - v < 0$ there are two equilibria (in the intervals $(0,x^*)$ and (x^*,∞), respectively). This condition is equivalent to $v > x^* - g(x^*)$. If $v = x^* - g(x^*)$, there is exactly one equilibrium at $x = x^*$; if $v < x^* - g(x^*)$, then there are no positive equilibrium points and all solutions go to extinction, which completes the proof. $\square$

Remark 1. Conclusions of Theorem 1 remain valid, if (A2) is replaced by (A2*).

Corollary 1.1. *If* $v > 0$, *then there is the only positive equilibrium for any r. Further, let* $v < 0$. *If* $r \leqslant 1$, *then* (12) *has no positive equilibrium points. If* $r > 1$ *and*

$$v < v^* = x^* - rx^* e^{-x^*}, \tag{16}$$

where x^* *is a solution of*

$$r(1 - x^*) = e^{x^*}, \tag{17}$$

then (12) *has no equilibrium points. If* $v = v^*$, *where* v^* *is defined in* (16), *then there is the only positive equilibrium point. If* $v > v^*$, *then there are two positive equilibrium points.*

Corollary 1.2. *By Remark* 1, *if* $v > 0$, *then* (15) *has the only positive equilibrium. If* $v < 0$ *and either* $r < 1$ *or for* $x^* = K(r-1)/(2r)$ *we have* $v < x^* - rx^*(1 - x^*/K) = -K(r-1)^2/(4r)$, *then all solutions represent extinction. Let* $r > 1$. *If* $v = -K(r-1)^2/(4r)$, *then there is a unique positive equilibrium. If* $v > -K(r-1)^2/(4r)$, *then there are two positive equilibrium points.*

Remark 2. Corollaries 1.1 and 1.2 present sufficient extinction conditions which generalize conditions of immediate extinction (Propositions 1 and 2, item 1, in [23]).

Now let us proceed to positiveness and stability conditions. First consider the case $v > 0$. Then all solutions are positive; moreover, $x_n > v$ for any $x_0 > 0$. Let us note that all proofs (without loss of generality) will be illustrated by examples of the Ricker model.

Theorem 2. *Suppose* (A1)–(A3) *hold,* $v > 0$ *and*

$$|g'(x)| \leqslant \lambda < 1, \quad x > c. \tag{18}$$

Then the only equilibrium point N^* *of* (5) *is a global attractor for all* $x_0 > 0$.

Proof. Function $f(x) = g(x) + v$ increases for $x < c$ and decreases for $x > c$. By Theorem 1 there is the only positive equilibrium point N^*. Let us consider three cases: $N^* = c$, $N^* < c$ and $N^* > c$ (we recall that $x = c$ is the maximum point of $f(x)$).

Let $N^* = c$ (see Fig. 1(left), $c = 1$). Then for any $x_0 \neq c$ we have $x_1 = f(x_0) < c$, for any $i \geqslant 2$ and $x_{i-1} < c$

$$c = N^* > x_i = f(x_{i-1}) > x_{i-1}.$$

The increasing bounded above sequence $\{x_n\}$ has a limit α. Taking the limit of $x_{i+1} = f(x_i)$ as $i \to \infty$ we obtain $\alpha = f(\alpha)$, i.e., α is the only equilibrium point N^* which is thus a global attractor: $\lim_{n \to \infty} x_n = N^*$ for any $x_0 > 0$.

Let $N^* < c$ (see Fig. 1(right), $c = 1$). Let $N_1 > c$ be a point, such that $f(N_1) = N^*$. Such $N_1 > N^*$ exists and is unique, since $f(c) > N^*$ ($f(x)$ is increasing, $x < c$) and $\lim_{x \to \infty} f(x) = v < N^*$. If $x_0 < N^*$, then $N^* > x_1 = f(x_0) > x_0$, $N^* > x_2 > x_1$, $N^* > x_n > x_{n-1}$; we have an increasing bounded sequence

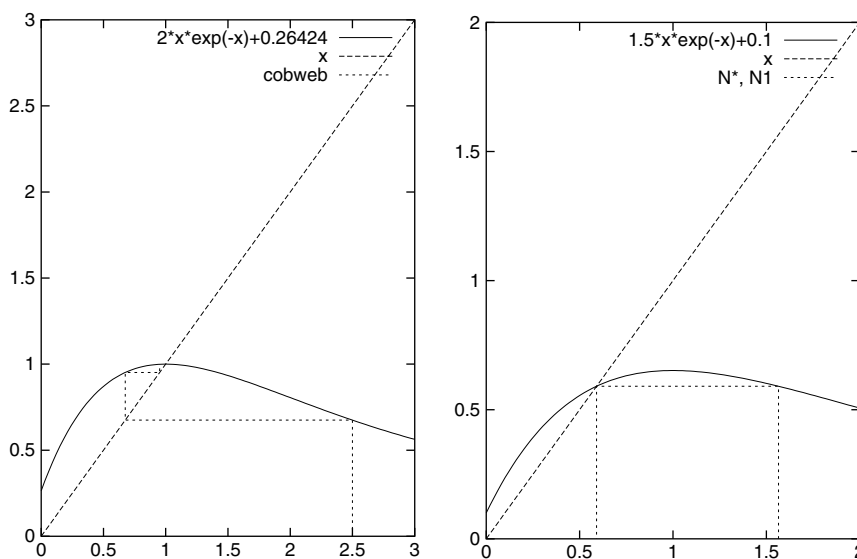Fig. 1. The reproduction curve $f(x) = 2xe^{-x} + 0.26424$ ($N^* \approx c = 1$) with some cobwebs (left) and $f(x) = 1.5xe^{-x} + 0.1$ with $N^* < c = 1$ with N_1 marked (right).

which tends to N^* from below. If $x_0 > N_1$, then $x_1 = f(x_0) < N^*$ and, beginning with x_1, we have the previous case. If $N^* < x_0 < N_1$, then $N^* < x_1 < c$, $x_2 = f(x_1) < x_1$, $N^* < x_2 < c$, we have a decreasing bounded sequence $\{x_n\}$ which tends to N^* from above. We have proven that eventually we have either an increasing sequence $0 < x_n < N^*$ or a decreasing sequence $N^* < x_n < c$, in both cases the sequence is convergent to N^*.

Finally, let $N^* > c$ and $|g'(x)| < 1$ for $x > c$ (see Fig. 2). Let us prove that for any x_0 for some k we have $c \leqslant x_n \leqslant 2N^* - c$, $n > k$. Let us define $N_1 \neq N^*$ as in the previous case: $f(N_1) = N^*$. If $N_1 < x_0 < N^*$, then $x_1 > N^*$. Consider $x_2 = f(x_1)$. For any $x > c$ there exists ζ, $c < \zeta < x$, such that $|x_{k+1} - N^*| = |f(x_k) - f(N^*)| = |f'(\zeta)||x_k - N^*| < |x_k - N^*|$. If $c < x_0 < N^*$, then $x_1 - N^* < N^* - x_0$ and $N^* - x_2 < x_1 - N^* < N^* - x_0$. Thus $c < x_2 < 2N^* - c$, the same is valid for $x_3, x_4, \ldots$ (each next point is closer to N^*).

If $N_1 < x_0 < c$, then there exists $x_0^*, c < x_0^* < N^*$, such that $f(x_0^*) = f(x_0)$, and the same argument as above implies $c < x_1 < 2N^* - c$, $c < x_2 < 2N^* - c, \ldots$ Thus the segment $[c, 2N^* - c]$ is mapped onto itself and if $c < x_0 < N^*$, then x_1 belongs to the segment. If $0 < x_0 < N_1$, then $x_1 > x_0$, we have a set of increasing first points, at some step j we have $N_1 < x_j < c$, so $x_k \in [c, 2N^* - c]$, $k = j + 1, j + 2, \ldots$. If $x_0 > 2N^* - c$, then $0 < x_1 < c$, which leads to the previous case. We have proven that for any x_0 for some k we have $c \leqslant x_n \leqslant 2N^* - c$, $n > k$. In addition $|f'(x)| = |g'(x)| < \lambda < 1$ for $x \in [c, 2N^* - c]$. The reference to Lemma 1 completes the proof. $\square$

Corollary 2.1. *Let* $v > 0$ *and*

$$r < e^2. \tag{19}$$

Then the only equilibrium point N^* *of* (12) *is a global attractor for all* $x_0 > 0$.

Proof. The first derivative of g is decreasing for $x < 2$, attains its minimum at $x = 2$ (which is $|f'(2)| = re^{-2} < 1$, when $r < e^2$) and then increases and tends to zero at infinity. Thus $|f'(x)| \leqslant \lambda = |f'(2)| < 1$ for any $x > 1$. $\square$
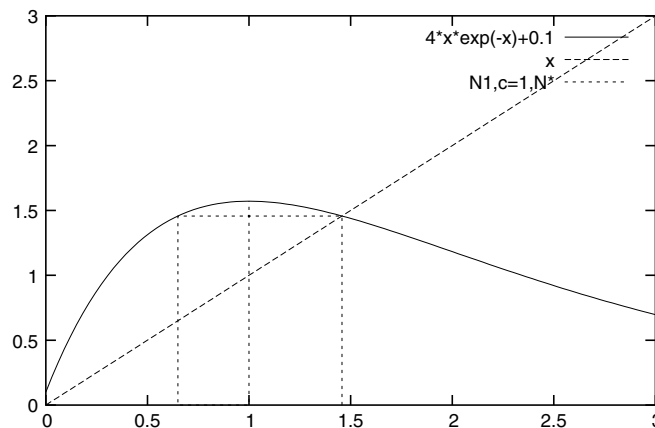

Fig. 2. The reproduction curve of the function $f(x) = 4xe^{-x} + 0.1$, $N^* > c = 1$.

Remark 3. In 1976, Levin and May [14] formulated the following conjecture: for some difference equations (including Ricker's delay equation) the local stability of the equilibrium implies its global stability. Theorem 2 and Corollary 2.1 partially confirm this hypothesis for some general model including the non-delayed impulsive difference Ricker's equation with constant recruitment (we note, that, in spite of the requirement $|f'(x)| < 1$ for $x > c$, the interval (c, ∞) can be reduced to any neighbourhood of the only equilibrium point). Recently this conjecture was revisited in [16], where the stability of equation $x_{n+1} = x_n F(x_{n-k})$ was studied.

Now let us proceed to the case $v < 0$. According to Theorem 1, there are 3 possible cases: no equilibrium points, the only equilibrium point N^* and two equilibrium points $N_1^* < N_2^*$. We will also introduce the following characteristic points:

$$N_3 : f(N_3) = N_1^*, \quad \text{where } f(N_1^*) = N_1^*, \ N_3 \neq N_1^* < N_2^*, \tag{20}$$

$$N_4 : f(N_4) = N_2^*, \quad \text{where } f(N_2^*) = N_2^*, \text{ or } f(N_4) = N^* = f(N^*). \tag{21}$$

Such points exist, since for $v < 0$ function $f(x)$ takes the value m, $0 \leqslant m < f(1)$, exactly twice on the halfline $(0, \infty)$. Besides, the maximum point $x = c$ is between N_1^* and N_3, between N_2^* and N_4 unless $N_2^* = c$: in this case $N_4 = N_2^* = c$. If $N_2^* \neq c$, we assume $N_4 \neq N_2^*$.

Theorem 3. *Suppose $v < 0$, (A1)–(A3) hold and $|g'(x)| \leqslant \lambda < 1$ for any $x > c$.*

(1) *If there is no positive equilibrium point, then any solution goes to extinction after a finite number of steps.*
(2) *If there is only the equilibrium N^*, then any solution with $N^* \leqslant x_0 \leqslant N_4$ tends to N^*, any solution with $x_0 < N^*$ or $x_0 > N_4$ goes to extinction after a finite number of steps.*
(3) *Suppose there are two positive equilibrium points $N_1^* < N_2^*$. Then any solution with $N_1^* < x_0 < N_3$ tends to N_2^* as $n \to \infty$. If $x_0 < N_1^*$ or $x_0 > N_3$, then the solution goes to extinction after a finite number of steps.*

Proof. (1) We have $g(x) + v < x$, so the sequence x_n is monotone decreasing. Since there is no positive (or even zero) equilibrium, then the solution becomes negative after a finite number of steps.

(2) For one positive equilibrium $g(x) + v < x$ if $x \neq N^*$. So all solutions are decreasing and for $x_0 < N^*$ become negative after a finite number of steps (see Fig. 3(left)). If $x_0 > N_4$, where $N_4 \neq N^*$ and $f(N_4) = N^*$, then $x_1 < N^*$ and we also have extinction after some steps.

Now let $N^* < x_0 < N_4$ (if $x_0 = N^*$ or $x_0 = N_4$ we have $x_i = N^*$, $i \geqslant 1$). Then $x_1 = f(x_0) < f(c) < c$ and $x_1 > N^*$. Since $f(x)$ is increasing in $[N^*, c]$ and is less than x, then all $x_i > N^*$, $i \geqslant 1$, $x_i < x_{i+1}$. The monotone decreasing bounded below sequence tends to equilibrium N^*.

(3) Now suppose there are two positive equilibria $N_1^* < N_2^*$. There are three possible cases: $N_2^* < c$, $N_2^* = c$ and $N_2^* > c$.

(a) Let $N_2^* < c$. Then (see Fig. 3 this (right)) for $x_0 < N_1^*$ the solution is decreasing and becomes negative; for $x_0 > N_3$ we have $x_1 < N_1^*$, so the solution goes to extinction. For $N_1^* < x_0 < N_2^*$ we get a monotone increasing solution which tends to the equilibrium N_2^*. The case $N_4 < x_0 < N_3$ gives $N_1^* < x_1 < N_2^*$ and thus the solution also tends to N_2^*.
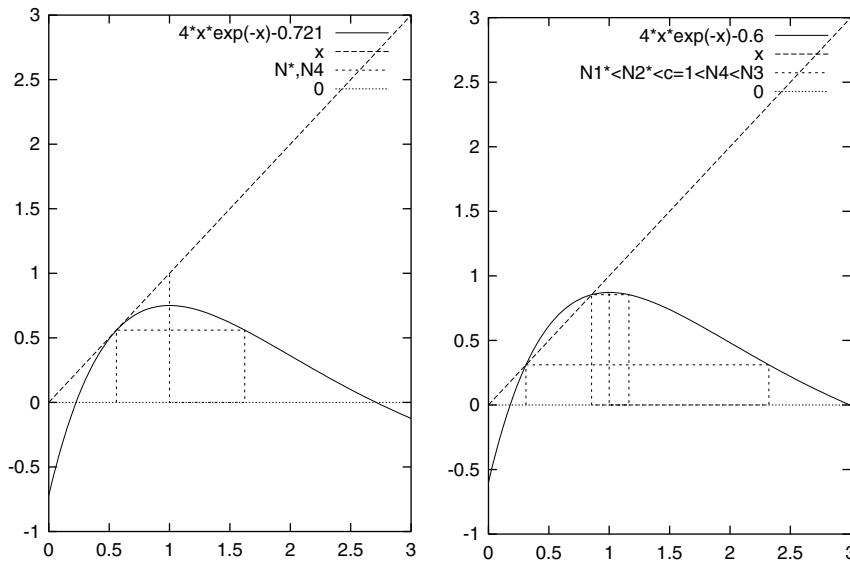
Fig. 3. The reproduction curve $f(x) = 4xe^{-x} - 0.721$ (left), with one positive equilibrium, and $f(x) = 4xe^{-x} - 0.6$ (right), with two positive equilibria, both less than the critical point $c = 1$.

 If $N_2^* < x_0 < c$, then the solution is decreasing ($f(x) < x$), exceeds N_2^* and tends to N_2^*. For $c < x_0 < N_4$ we have $N_2^* < x_1 < c$, so the solution also tends to the equilibrium.

(b) Let $N_2^* = c$. Then for any $x_0 < N_1^*$ or $x_0 > N_3$ the solution goes to extinction (see Fig. 4(left)), the proof is similar to the previous case. For any $N_1^* < x_0 < N_3$ we have $N_1^* < f(x_0) < c$. Any solution with $x_0, N_1^* < x_0 < c$, is increasing and tends to N_2^*.

(c) Let $N_2^* > c$. The extinction for $x_0 < N_1^*$ or $x_0 > N_3$ is proven as in the previous cases (see Fig. 4(right)). Let us introduce $N_5 \neq c$, such that $f(N_5) = c$ and prove that for any $x_0, N_1^* < x_0 < N_3$ there is such n that $x_i \in [c, N_5]$, $i > n$. We have $N_1^* < N_4 < c < N_2^* < N_5 < N_3$. If $x_0 \in (N_1^*, N_4]$, then the solution eventually becomes greater than c, since $c < N_2^*$. If $x_0 \in [N_2^*, N_3)$, then $x_1 \in (N_1^*, N_4]$, which is the previous case. If $x_0 \in [N_4, c]$, then (see Fig. 4(right)) $x_1 = f(x_0) \in [N_2^*, f(c)]$.

 Now we prove that f maps the attracting segment $[c, f(c)]$ onto itself. For $c \leqslant x_0 \leqslant N_2^*$ we have $N_2^* \leqslant x_1 \leqslant f(c)$. Let us show that for $N_2^* \leqslant x_0 \leqslant f(c)$ we have $x_1 \geqslant c$. In fact, for some $\zeta, N_2^* < \zeta < c, N_2^* - f(x_0) = N_2^* - x_1 = f'(\zeta)(N_2^* - x_0) < x_0 - N_2^*$, since $|f'(x)| < 1$ for any $x > c$ by the hypothesis of the theorem. On the other hand, $f(c) - N_2^* < N_2^* - c$ (in Fig. 4 this (right) in the upper triangle the vertical leg is less than the horizontal one since $|f'(x)| < 1$, while in the lower triangle the legs are equal). Thus $N_2^* - x_1 \leqslant x_0 - N_2^* \leqslant f(c) - N_2^* \leqslant N_2^* - c$ implies $x_1 \geqslant c$. The inequality $x_1 \leqslant f(c)$ is obvious, since $f(c)$ is the global maximum of $f(x)$, consequently, f maps $[c, f(c)]$ onto itself. Besides, $|f'(x)| < 1$ for $x \in [c, f(c)]$. Application of Lemma 1 completes the proof of the theorem. $\square$

Corollary 3.1. *Let $v < 0$, $r < e^2$. If $r < 1$ or $r \geqslant 1$ and $v < v^*$, where v^* is defined in (16), (17), then all solutions of (12) extinct. If $v = v^*$, then all solutions with $N^* \leqslant x_0 \leqslant N_4$ converge to N^*, all other*
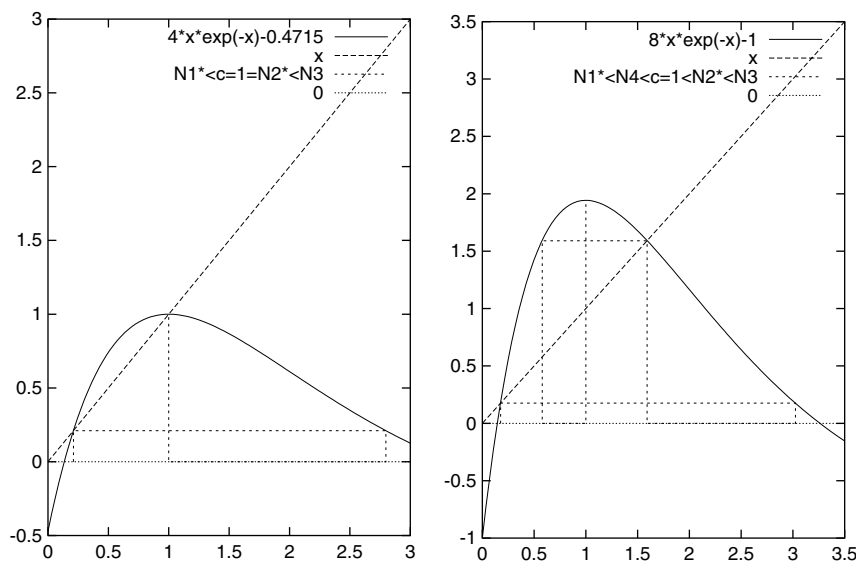
Fig. 4. The reproduction curve $f(x) = 4xe^{-x} - 0.4715$ (left), with two equilibria $N_1^* < c = 1$ and $N_2^* = c$, and $f(x) = 8xe^{-x} - 1$ (right), with two equilibria $N_1^* < c = 1 < N_2^*$.

solutions extinct. If $v > v^*$, then all solutions with $N_1^* \leqslant x_0 \leqslant N_3$ converge to N_2^*, all other solutions extinct.

Remark 4. Conclusions of Theorems 2 and 3 remain valid if conditions (A2) and (18) are changed by the following:

(A2*) is satisfied and there exists λ, $0 < \lambda < 1$, such that $|g(x) - g(y)| < \lambda|x - y|$ for $x, y > c$.

3. Ricker model with variable coefficients

We consider the perturbed Ricker model with variable coefficients

$$x_{n+1} = r_n x_n e^{-x_n} + v_n \tag{22}$$

under the assumptions that for any n either $v_n > 0$ or $r_n > 1$ and the inequality

$$v_n > v^*(r_n) = x_n^* - r_n x_n^* e^{-x^*}, \tag{23}$$

holds, where x_n^* is a solution of the equation

$$r_n(1 - x_n^*) = e^{x_n^*}. \tag{24}$$

If this assumption is not satisfied for $n = k$, then the kth generation may be the last one due to excessive depletion rate at kth step. Under these assumptions for each n there is a positive

equilibrium point. For $v_n < 0$ there are two positive equilibria, while for $v_n > 0$ there is only one.

Let us introduce the following notation:

$$f_n(x) = r_n x e^{-x} + v_n \tag{25}$$

and further consider equilibria and other characteristic points of the equations (with constant coefficients):

$$x_{k+1} = f_n(x_k) = r_n x_k e^{-x} + v_n, \quad k = 0, 1, 2, \ldots, \tag{26}$$

such as:

$N_1^*(r_n, v_n)$ is the smallest positive equilibrium point (which exists for $v_n < 0$ only);
$N_2^*(r_n, v_n)$ is the greatest positive equilibrium point (the only one for $v_n > 0$);
$N_3(r_n, v_n)$ is also defined for $v_n < 0$ only as the point $N_3(r_n, v_n) > N_1^*(r_n, v_n)$, such that we have $f_n(N_3(r_n, v_n)) = N_1^*(r_n, v_n)$;
$N_{3,\min} = \inf_n N_3(r_n, v_n)$, $N_{1,\max} = \sup_n N_1(r_n, v_n)$,
$r_{\max} = \sup_n r_n$, $r_{\max}^+ = \sup\{r_n | v_n > 0\}$,
$r_{\min} = \inf_n r_n$, $r_{\min}^- = \inf\{r_n | v_n < 0\}$,
$v_{\max} = \sup_n v_n$,
$v^*(r)$ is defined by (23) and (24).

Certainly $N_{3,\min}$, $N_{1,\min}$ take into account steps with depletion only. Let us also note that $v^*(1) = 0$.

Remark 5. $N_2^*(r, v)$ is an increasing function in both r and v. For negative v, $N_1^*(r, v)$ is a decreasing function in both r and v.

Theorem 4. *Suppose* $r_{\min} \geqslant 1$, $r_{\max} < \infty$, $v_{\max} < \infty$,

$$r_n < e^2, \tag{27}$$

$$v_n > v^*(r_{\min}) \tag{28}$$

for any n, where $v^*(r)$ *is defined by* (23), (24), *and*

$$\frac{r_{\max}^+}{e} + v_{\max} < N_{3,\min}. \tag{29}$$

Then for any x_0 *satisfying inequalities*

$$N_{1,\max} < x_0 < N_{3,\min} \tag{30}$$

the solution of (22) *is bounded and persistent and is asymptotically attracted by the segment*

$$[N_2(r_{\min}, v_{\min}), N_2(r_{\max}, v_{\max})]. \tag{31}$$

Proof. Inequality (27) implies that for $v_n < 0$ we have $f_n(f_n(1)) = N_1^*$, so the segment $[N_1^*(r_n, v_n), f_n(1)]$ is an immediate attraction basin for any $x_n \in [N_1^*(r_n, v_n), N_3(r_n, v_n)]$. By condition (28) there is no immediate extinction at a certain step and N_1^*, N_3 are defined at any step, where $v < 0$. If $v > 0$, then $[N_1^*(r_n, v_n), f_n(1)]$ is an immediate attraction basin for any x_n. Finally, (29) yields that the immediate attraction basin for f_{n-1} includes only points of attraction of the positive equilibrium $N_2^*(r_n, v_n)$ for the next mapping. Thus, if we take the initial point in the intersection of all points attracted by positive equilibria (30), then the solution is persistent (exceeds $N_{1,\min}$) and is bounded (does not exceed the maximal value of f which is $r_{\max}^+/e + v_{\max}$). The solution is attracted by the variety of positive attractors which is a subset of (31). $\square$

Corollary 4.1. *If $v_n > 0$ and r_n are bounded, then for any initial condition the solution of (22) is persistent and bounded.*

Remark 6. If $v_n = 0$, then the solution is not necessarily persistent (even for constant r, if r is in the 'chaos area').

Now let us consider the case of periodic r_n, v_n. Periodicity of parameters is usually explained by seasonal changes in the environment, low survival rates in winter, changing reproduction rates and migrations at certain times of the year.

Theorem 5. *Suppose r_n and v_n are periodic with period l*

$$r_{n+l} = r_n, v_{n+l} = v_n \tag{32}$$

and for v_n, r_n, $1 \leqslant n \leqslant l$, the conditions of Theorem 4 hold. Then there exists a positive periodic solution of Eq. (22).

Proof. Under the assumptions of Theorem 4 the non-empty segment $[N_{1,\max}, N_{3,\min}]$ is mapped onto itself by any f_n. Thus the composition of mappings $f_0, f_1, \ldots, f_{l-1}$ is continuous and maps $[N_{1,\max}, N_{3,\min}]$ onto itself. Thus it has fixed point x_0^*. Then $x_0^*, x_1^* = f_0(x_0^*), x_2^* = f_1(x_1^*), \ldots, f_{l-1}(x_{l-1}^*) = x_0^*, x_1^*, \ldots$ is a periodic solution of (22). $\square$

4. Discussion

First let us discuss biological relevance of conditions (A1)–(A3). (A1) claims the positiveness of the reproduction function for any size of the population and the zero value in the absence of a population; in addition, there is a restriction that overpopulation leads to a small population size at the next time step (this can take into account pollution or limited resources incorporated with their uniform distribution). In (A2) it is assumed that there is some point c leading to the maximal population size. Population increases for small sizes and decreases for large sizes. Moreover, according to (A3), for very small sizes of the population the rate of increase is the highest. Overall, this can represent a system in which density dependence occurs through scramble competition [4] (resources are divided evenly among competing individuals). To the best of our knowledge, the idea of density-dependent mortality in ecological models goes back to Nicholson [19] and Smith [25], though the Verhulst equation [30] already used the idea.

Further, let us refer to more general types of perturbations, such as random perturbations. In [27] the following problem was discussed: for which maps $f(r,d,x)$ the equation $x_{n+1} = f(r,d,x_n)$ has a stable two-cycle for $r \to \infty$ and fixed $d > 0$? If d is not constant but can take n positive values $d_1, d_2, \ldots, d_n$, what is the bifurcation diagram for $r \to \infty$? We recall that for

$$f_1(r,d,x) = x \exp\{r(1-x)\} + d \tag{33}$$

and d taking values $d_1, d_2, \ldots, d_n$ with non-zero probabilities, for $r \to \infty$ there are $n(n+1)$ limit blurred orbits, n corresponding to d_i and n^2 corresponding to transfers $f(r, d_j, d_i)$, $i, j = 1, 2, \ldots, n$ ([27], Theorem 2.1).

First let us describe the biological meaning of such behavior. Under very high growth rates, overpopulation leads to ecological disaster which results in very small levels of population at the next time step. Survival is mainly due to immigration at the level of d_i. There is a high population level corresponding to $f(r, d_j, d_i)$ at the next step etc.

Let us propose some sufficient conditions when there are limit two-cycle periods.

Claim. Suppose

(a1) $f(r,d,x) > 0$ for any $r > 0$, $d > 0$, $x > 0$;
(a2) there exist point $x^* > 0$ and function $\lambda(d)$, such that $0 < \lambda(d) < x^*$ and for fixed x, d

$$\lim_{r\to\infty} f(r,d,x) = \begin{cases} \infty, & 0 < x < x^*, \\ \lambda(d), & x > x^*. \end{cases} \tag{34}$$

Consider the difference equation

$$x_{n+1} = f(r,d,x_n) \tag{35}$$

and suppose in addition

(a3) d is a discrete random variable, with values $a_1, a_2, \ldots, a_n$, such that probabilities $P\{d_n = a_i, d_{n+1} = a_j\} > 0$ for any $i, j, \lambda(a_i) < x^*$ and for r large enough $f(r, a_j, \lambda(a_i)) > x^*$.

Then for $r \to \infty$ the asymptotes of the $n(n+1)$ blurred orbits are $\lambda(a_i)$ and $f(r, a_j, \lambda(a_i))$, $i, j = 1, 2, \ldots, n$.

We suggest that the proof of this claim follows the proof of Theorem 2.1 in [27]. Another observation is that with the growth of n the diagram will be more and more similar to the chaotic behavior. However, if $\min_i \lambda(a_i) > 0$, we will have persistence of solutions. This claim partially gives an answer to the problem stated in [27].

Let us present examples of curves which can lead to $n(n+1)$ limit two-cycle periods for large r. Everywhere below we assume $d = a_1, a_2, \ldots, a_n$, where (a3) is satisfied.

Example 3. As well known [26,27], for

$$x_{n+1} = x_n \exp\{r(1-x_n)\} + d \tag{36}$$

there are limit two-cycle periods for r large enough. Examples of relevant bifurcation diagrams for (36) with d random can be found in [27]. The same is valid if some $a_i = 1$. In numerical simula-

tions, the following behavior of solutions was discovered for the constant coefficient Eq. (36) with $d > 1$. For certain r there is a stable two cycle. The two values draw closer with the growth of r, not differ much from the stable equilibrium point for large r. This means that the immigration level is so high that it leads to overpopulation and extinction of the local population at the next step, so the population at each step is close to the number of immigrating species.

Example 4. The modified truncated logistic map $f_2(r,d,x) = \max\{rx(1-x),0\} + d$, under the assumption $a_i < 1$, satisfies (a1), (a2) of the claim. In Fig. 5 the following bifurcation diagrams are presented: for $d = 0.3$, 0.6 (left) with 6 limit orbits and for $d = 0.067$, 0.133, 0.2 with $3 \cdot (3 + 1) = 12$ limit orbits.

In the stream of the study of random perturbations, we suggest the following open questions:

1. For a given constant depletion, for the growth rate $r > r^*$ extinction is inevitable for unimodal maps with negative Schwarzian derivative [23]. For random perturbation rates, which type of models has the following property: if d takes a negative value with a non-zero probability, then there is the growth rate r^*, such that for $r > r^*$ population goes to extinction with probability one?
2. Describe sufficient non-extinction conditions for truncated logistic and generalized Beverton Holt maps with variable parameters (similar to Theorem 4 for the Ricker map). For constant coefficients and random perturbations (including negative values) deduce extinction probabilities.
3. We believe that the conclusion of the claim is applicable for perturbed models of contest competition (where the original reproduction rate satisfies $\lim_{x\to\infty} g(x) = K > 0$). Which results of Section 2 will hold for the perturbed contest competition?
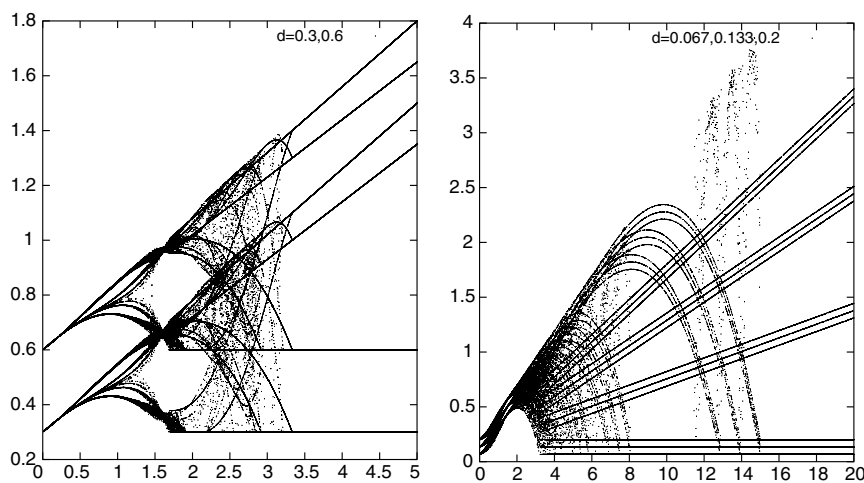

Fig. 5. Bifurcation diagrams for the truncated logistic map with random migration d: $d = 0.3$, 0.6 (left) with 6 limit orbits and $d = 0.067$, 0.133, 0.2 (right) with 12 limit orbits.

Acknowledgments

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