STABILITY ANALYSIS OF PERIODIC FOX PRODUCTION MODELS

LEV IDELS

ABSTRACT. In this paper we introduce a nonlinear Fox surplus production model in a periodic environment

\[
\frac{dN}{dt} = r(t) \left( \ln \frac{K(t)}{N(t)} \right)^\theta - F(t) N(t).
\]

The existence and stability of the periodic solutions of nonautonomous nonlinear differential equation (A) are analyzed. Sufficient conditions are obtained for the global attractivity of positive periodic solutions. Our results extend those the well-known results recently obtained by Brauer \cite{2} for a periodic Gompertzian model. We study the combined effects of periodically varying carrying capacity, inherent growth rates, and periodic harvesting of the population. Some numerical simulations illustrate how the Fox model is able to capture the trend in the data for Pacific Ocean perch obtained by the Pacific Biological Station (Nanaimo, BC).

1 Introduction Ecosystem effects and environmental variability are very important factors \cite{4, 5, 13–15}, and mathematical models cannot ignore for example, year-to-year changes in weather, habitat destruction and exploitation, the expanding food surplus, and other factors that affect the population growth. According to \cite{14} “the effects of a periodically varying environment are also an important factor in laboratory ecosystems where the feeding pattern may influence the population.” This paper was inspired by the results recently obtained by Brauer \cite{2} for Gompertz model with periodic parameters. The organization of this paper is as follows. In Section 2 we discuss the biological motivation of the \(\theta\)-Fox model with variable parameters. In Section 3 the existence and stability of the periodic solutions of nonautonomous

---

Research supported in part by a grant from the Natural Sciences and Engineering Research Council of Canada.

Keywords: Population models, nonautonomous differential equations, harvesting strategies, Gompertz model, Fox production model, stability.

Copyright ©Applied Mathematics Institute, University of Alberta.
nonlinear differential equations are considered, and sufficient conditions were obtained for the global attractivity of positive periodic solutions. Along with qualitative studies, in Section 4 numerical simulations are used to discuss the Fox model, the general logistic model and recent fisheries data. The interior-reflective Newton method was used to efficiently estimate the parameters of the Fox model.

2 Fox surplus production model (the biological foundation of the model) Consider the following canonical differential equation of Population Dynamics

\[
\frac{dN}{dt} = [G(t, N) - F(t)]N(t)
\]

where \( N = N(t) \) is the population biomass, \( G(t, N) \) is the per-capita fecundity rate, and \( F(t) \) is the per-capita rate of depletion (the per-capita mortality rate due to natural mortality causes and harvesting). In equation (1) let \( G(t, N) \) be a Gompertz type function

\[
G(t, N) = r(t) \left( \ln \frac{K}{N} \right)^\theta
\]

for \( \theta > 0 \), then equation (1) takes a form

\[
\frac{dN}{dt} = N(t) \left[ r(t) \left( \ln \frac{K(t)}{N(t)} \right)^\theta - F(t) \right]
\]

where \( r(t) \) is an intrinsic factor, \( F(t) \) is a harvesting factor, and \( K(t) \) is a varying environmental carrying capacity. Parameter \( \theta \) is referred to as an interaction parameter: if \( \theta > 1 \), then intra-specific competition is high, and if \( 0 < \theta \) is less than 1, the competition is lower. Equation (2) is called a Fox surplus production model, and has been used to build up prediction models for multitudinous use [10, 11, 17], e.g., in microbial growth models, demographic models, evolution biology models, fisheries models, etc. For \( \theta = 1 \) equation (2) is a classical Gompertzian model [1, 7]

\[
\frac{dN}{dt} = \left[ r(t) \ln \frac{K}{N} - F(t) \right] N(t).
\]

This equation is an alternative to the logistic model

\[
\frac{dN}{dt} = \left[ r(t) \left( 1 - \frac{N}{K} \right) - F(t) \right] N(t).
\]
It is well-known that the logistic curve has equal periods of slow and fast growth. In contrast, the Gompertzian curve does not incorporate the symmetry and has a shorter period of fast growth. The Fox model is better than a traditional logistic model, especially when the actual data follows a smooth curve \[5, 15, 16\]. The Fox model (2) is an alternative to the \(\theta\)-logistic model \[16\]

\[
\frac{dN}{dt} = r(t) \left(1 - \left(\frac{N}{K}\right)^\theta\right) - F(t) N(t).
\]

Note also that the Fox model becomes more important at a lower population density than that with the \(\theta\)-logistic model \[5, 15\].

### 3 Fox model with variable parameters

Consider equation (2) where \(r(t)\) and \(F(t)\) are positive continuous functions for all \(t > 0\) and \(r(t) > F(t)\). The function \(K(t)\) is positive and continuously differentiable for all \(t \geq 0\). A new variable \(v(t) = \ln(K(t)/N(t))\) transforms equation (2) to a nonlinear differential equation

\[
\dot{v} + r(t)v^\theta = F_1(t)
\]

with \(F_1(t) = F(t) + (K'(t)/K(t))\). If \(\theta = 1\) (Gompertzian model), equation (4) is a linear differential equation, and the solution can be expressed in the form

\[
v(t) = a(t) \int_0^t \frac{F_1(s)}{a(s)} ds,
\]

where

\[
a(t) = \exp \left(-\int_0^t r(s) ds\right).
\]

Brauer \[2\] has studied the Gompertzian model (3) and proved that if all functions \(r(t)\), \(K(t)\) and \(F(t)\) are \(T\)-periodic functions, and \(F(t) < r(t)K(t)/e\), then equation (3) has a globally stable periodic solution with an initial value between \(K(0)/e\) and \(K(0)\). The technique used in \[2\] depends on the existence of the explicit form (5) of the solution to equation (3). If \(\theta = 2\), then equation (4) is a well-known Riccati equation \[9\]. Note that equation (4) is not analytically solvable for an arbitrary constant \(\theta > 0\).
Remark 1. If all parameters in equation (2) are constants, then equation (2) has one asymptotically stable equilibrium point

\[ N_e = K \exp \left( -\frac{F}{r} \right) \].

In general, nonautonomous differential equations do not have equilibrium solutions, and qualitative analysis is replaced by the problems of existence and stability of the solutions.

We prove the following results for equations (2) and (4).

**Theorem 3.1.** Suppose that:

(B) \[ F_1(t) = F(t) + \frac{K'(t)}{K(t)} > 0 \quad \text{and} \quad 0 < N(0) < K(0). \]

Then the solution of equation (2) exists for all \( t \geq 0 \) and \( 0 < N(t) < K(t) \).

**Proof.** Consider equation (2). Clearly, \( N(t) > 0 \). Suppose \( t = t_1 \) is the first point where \( N(t_1) = K(t_1) \). The change of variables

\[ v(t) = \ln \frac{K(t)}{N(t)} \]

transforms equation (2) to equation (4) for \( t \in [0, t_1] \). By assumption (B) \( F_1(t) > 0 \). A substitution \( q(t) = r(t)v^{\theta-1}(t) \) into (4) yields

(6) \[ \dot{v} + q(t)v = F_1(t). \]

The solution of (6) can be expressed in the following form

(7) \[ v(t) = v(t, 0) \left[ v(0) + \int_0^t v(t, s)F_1(s)ds \right], \]

where \( v(t, s) \) is the fundamental function of linear equation (6) with

\[ v(0) = \ln \frac{K(0)}{N(0)} > 0. \]

If \( N(t_1) = K(t_1) \),
then $F_1(t) > 0$, $v(t, 0) > 0$. Hence $v(t) > 0$ for $t \in [0, t_1)$. Thus we have a contradiction and therefore $0 < N(t) < K(t)$.

If $N(t) > 0$ is not a global solution of equation (2), then there exists $t_2 > 0$ such that

$$\lim_{t_1 \to t_2} N(t) = \infty.$$ 

But $N(t) < K(t)$, therefore

$$\lim_{t_1 \to t_2} N(t) < K(t_2) < \infty$$

yields $N(t)$ is a global solution of (2). \qed

To prove our next theorems we will use [2, 12].

**Lemma 3.1 (Friedrichs Theorem).** Suppose that $G(t, N)$ is a smooth function with period $T$ in $t$ for every $N$. Suppose also that there exist constants $a, b$ with $a < b$ such that $G(t, b) < 0 < G(t, a)$ for every $t$. Then there is a periodic solution $N_0(t)$ of the differential equation $dN/dt = G(t, N)$ with period $T$ and $N(0) = c$ for some $c \in (a, b)$.

**Lemma 3.2 (Lazer-Sanchez Theorem).** Suppose that $G(N)$ is a smooth function and $H(t)$ is periodic with period $T$. Then the differential equation $dN/dt = G(N) - H(t)$ has at most two periodic solutions of period $T$ in any interval on which $G''(N) \neq 0$.

**Theorem 3.2.** Consider equation (2) for $\theta > 0$ with positive $T$-periodic functions $r(t)$, $K(t)$ and $F(t)$. For all $t \geq 0$ we assume:

(A1) \hspace{1cm} $F_1(t) > 0$.

Then there exists a positive periodic solution $N_0(t)$ such that $K(0)e^{-b} < N_0(0) < K(0)$, $0 < N_0(t) < K(t)$ where $b$ is a constant defined as

$$b = \max_{0 \leq t \leq T} \left( \frac{F_1(t)}{r(t)} \right)^\frac{1}{p}.$$

If additionally we assume:

(A2) \hspace{1cm} $r(t) = r_0 > 0$,

then equation (2) has at most two periodic solutions.
Proof. Inserting \( v(t) = \ln(K(t)/N(t)) \) into (2) yields equation (4). Denote
\[
G(t, v) = -r(t)v^\theta + F_1(t).
\]
It can readily be seen that \( G(t, 0) > 0 \) and \( G(t, b + \varepsilon) < 0 \) for every \( \varepsilon > 0 \). Therefore, based on Lemma 3.1 for equation (4), there exists a periodic solution \( v_0(t) \) such that \( 0 < v_0(0) < b + \varepsilon \). Since \( \varepsilon \) is an arbitrary number, \( 0 < v_0(0) \leq b \). Therefore, \( N_0(t) = K(t)e^{-v_0(t)} \) is a periodic solution of equation (2) such that
\[
K(0)e^{-b} < N_0(0) < K(0).
\]
Theorem 3.1 implies also that \( N_0(t) < K(t) \). If the extra condition (A2) is assumed, then equation (4) transforms to
\[
\frac{dv}{dt} = -rv^\theta + F_1(t) = R(v) + F_1(t).
\]
Clearly, \( R(v) \) is satisfying all conditions of Lemma 3.2 and therefore equation (8), along with equation (2), has at most two periodic solutions.

Remark 2. If all functions \( r(t), K(t) \) and \( F(t) \) have different periods, then equation (2) has at least one almost periodic solution.

Lemma 3.3. Consider the following equation
\[
\frac{dv}{dt} + r(t)v^\theta = F(t).
\]
Assume that \( \theta > 0 \),
\[
0 < \liminf_{t \to \infty} F(t) \leq \limsup_{t \to \infty} F(t) < \infty,
\]
and
\[
0 < \liminf_{t \to \infty} r(t) = \limsup_{t \to \infty} r(t) < \infty.
\]
If \( v(t) \) is a positive solution of (9) for \( t \geq 0 \), then
\[
0 < \liminf_{t \to \infty} v(t) = \limsup_{t \to \infty} v(t) < \infty.
\]
Proof. Suppose that
\[ \liminf_{t \to \infty} v(t) = 0. \]
If
\[ \lim_{t \to \infty} v(t) = 0 \]
exists, then
\[ \lim_{t \to \infty} \left( \frac{dv}{dt} - F(t) \right) = 0. \]
Hence
\[ \liminf_{t \to \infty} \left( \frac{dv}{dt} \right) > 0. \]
Thus
\[ \lim_{t \to \infty} v(t) = \lim_{t \to \infty} \left[ v(0) + \int_0^t \frac{dv}{ds} \, ds \right] = \infty \]
and we have a contradiction. If \( \lim_{t \to \infty} v(t) \) does not exist, then there exists a sequence \( t_n \) such that \( t_n \to \infty \), \( v(t_n) \to 0 \), and \( \frac{dv}{dt}(t_n) = 0 \). Then the equality
\[ r(t_n)v(t_n) = F(t_n) \]
yields \( F(t_n) \to 0 \). This contradiction proves that \( \liminf_{t \to \infty} v(t) > 0 \).

Suppose now that
\[ \limsup_{t \to \infty} v(t) = \infty. \]
If there exists \( \lim_{t \to \infty} v(t) \), then
\[ \lim_{t \to \infty} \frac{dv}{dt} = -\infty, \]
and this leads to a contradiction.

\[ \square \]

**Theorem 3.3.** Suppose all conditions of Theorem 3.2 hold. Then a periodic solution \( N_0(t) \) of equation \( (2) \) with \( 0 < N_0(0) < K(0) \) is a globally asymptotically stable solution.

Proof. Suppose \( N_1(t) \) and \( N_2(t) \) are two positive solutions of equation \( (2) \) with \( 0 < N_i(t) < K(0), i = 1, 2 \). Then \( v_1(t) = \ln(K(t)/N_1(t)) \) and \( v_2(t) = \ln(K(t)/N_2(t)) \) are two positive solutions of the equation
\[ \frac{dv}{dt} = -r(t)v^\theta + F_1(t). \]
Without loss of generality, we assume that $0 < v_1(t) < v_2(t)$. Let $v(t) = v_2(t) - v_1(t)$. Then equation (10) takes the form

$$\frac{dv}{dt} = -r(t)[v_2^\theta(t) - v_1^\theta(t)].$$

Application of the Mean Value Theorem transforms equation (11) to

$$\frac{dv}{dt} = -b(t)v(t)$$

where function $b(t)$ satisfies the following inequalities:

$$\theta r(t)v_1^{\theta - 1} \leq b(t) \leq \theta r(t)v_2^{\theta - 1} \quad \text{if } \theta \geq 1$$

and

$$\theta r(t)v_2^{\theta - 1} \leq b(t) \leq \theta r(t)v_1^{\theta - 1} \quad \text{if } 0 \leq \theta < 1.$$ 

Lemma 3.3 implies that $\lim \inf_{t \to \infty} b(t) > 0$. The last inequality ensures

$$\int_0^\infty b(s) \, ds = \infty$$

and therefore we have $\lim \inf_{t \to \infty} v(t) = 0$ or $\lim \inf_{t \to \infty} [v_2(t) - v_1(t)] = 0$. Summing up, we conclude

$$\lim \inf_{t \to \infty} [N_2(t) - N_1(t)] = 0.$$  

Remark 3. If $N_1(t)$ and $N_2(t)$ are any two solutions of equation (2), then statement (12) is true without assuming that all functions $r(t)$, $K(t)$ and $F(t)$ are $T$-periodic.

4 Numerical simulations  It is shown in [5, 6] that the effect of the environmental cycles is “a very model-dependent phenomenon.” For numerical simulations several choices of $r$, $K$ and $F$ have been employed:

$$r(t) = r_0 + \beta \sin \left( \frac{2\pi t}{T_r} \right),$$

$$K(t) = K_0 + k_0 \sin \left( \frac{2\pi t}{T_K} \right).$$
For the harvesting rate we assume that a periodic function $F(t)$ is defined as $F(t) = 0$ if $0 \leq t < \varphi$ and

$$F(t) = F_0 \left[1 - \cos \left(\frac{2\pi t}{T_F}\right)\right],$$

if $\varphi \leq t \leq T_F + \varphi$, and $\varphi$ is a “start-up time” for harvesting. For simplicity, we assume that periods have a lowest common multiple, which defines the period for the system. Let us compare the Fox model and $\theta$-logistic model with the actual weekly tow-by-tow data for Pacific Ocean perch (POP), obtained by the Pacific Biological Station (Nanaimo, BC) in 1995–2004 (see Figures 1 and 2). The interior-reflective Newton method was used to efficiently estimate the parameters of the models. In our experiments we used $T_r = 2$, $T_K = 4$ and $T_F = 1$, $\varphi = 0.4$.

![Graph showing real data and fitted data for comparison.](image)

**FIGURE 1:** Gompertz general model and real data from the Pacific Biological Station.

It is clear from the graphs that the Fox model captures the trend in real data better than an alternative $\theta$-logistic model. Our results
indicate that the use of the Fox model to describe fisheries should be recommended because of its ability to fit experimental data.

FIGURE 2: $\theta$-logistic model and real data from the Pacific Biological Station.

Acknowledgment We wish to thank Dr. J. Schnute from the Pacific Biological Station (Nanaimo, BC) for supplying us with data. We also thank graduate student B. Ou (University of Victoria, BC) for the statistical analysis of the data.

REFERENCES


Department of Mathematics, Malaspina University-College,
900 Fifth St. Nanaimo, BC, Canada V9S 5J5

E-mail address: idels@mala.bc.ca